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CITATION:

SHIMADA, TOMOHIKO ...[et al]. A taxonomic study of Whitehead's torrent frog, Meristogenys whiteheadi, with descriptions of two new species (Amphibia: Ranidae). Zoological Journal of the Linnean Society 2011, 161(1): 157-183

ISSUE DATE:

2011-01-13

URL:

http://hdl.handle.net/2433/197182

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short running title: A taxonomic study of *Meristogenys whiteheadi* (Amphibia: Ranidae)

Number of text pages: 33
Number of figures: 8
Number of tables: 7

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A taxonomic study of Whitehead's torrent frog, *Meristogenys whiteheadi*, with description of two new species (Amphibia: Ranidae)

The genus *Meristogenys* (Anura: Ranidae), endemic to Borneo, presents serious taxonomic problems despite being one of the commonest frogs in the mountainous regions of this island. We investigated molecular and morphological variations in *M. whiteheadi* (Boulenger, 1887) using larval and adult specimens from Sabah and Sarawak (Malaysia). We found three allopatric lineages in this species. We regard each of these as a distinct species because they are separated by a large genetic distance and do not form any monophyletic group. Their morphological characters indicate that the distributional range of *M. whiteheadi sensu stricto* is divided into two disjunct areas, Mt. Kinabalu (northern Sabah) and northern Sarawak. The two other lineages occupy ranges between those of *M. whiteheadi* and represent undescribed cryptic species. One of these, *M. stigmachilus*, collected from the northern part of the Crocker Range, is distinguished from *M. whiteheadi* by black spots on the upper lip and dark dots scattered on the back. A second undescribed species, *M. stenocephalus*, was collected mainly from the southern part of the Crocker Range and is characterised by the large body size of males and a relatively narrow head. *Meristogenys stenocephalus* also differs from *M. stigmachilus* and *M. whiteheadi* in larval morphology, but larvae of the latter two cannot be differentiated morphologically. We discuss relative tibia length, a diagnostic specific characteristic in the genus *Meristogenys*, and the relationships between body size and sexual size dimorphism in this genus.

ADDITIONAL KEYWORDS: body size sexual dimorphism – Borneo – cryptic species – *Meristogenys*.

INTRODUCTION

Borneo Island, located in the Greater Sunda Islands in South-east Asia, is characterised by a highly endemic biota. Inger & Stuebing (2005) listed 148 Bornean anurans, while 91 (61.5%) of them are endemic to Borneo (Inger & Stuebing, 2005). However, the rate of endemic species is even higher than this value today, because quite a few new taxa have been described thereafter, all of which are considered to be endemic to this island (e.g. *Meristogenys maryatiae* Matsui *et al.*, 2009, *Philautus davidlabangi* Matsui, 2009). Based on the accumulated curve of species recorded in Sabah, smaller part of Borneo, Matsui (2006) surmised the total number of Bornean amphibian species to increase, and gave a pessimistic view that the time of completion in inventory cannot be estimated.

A genus of ranid frogs, *Meristogenys* Yang, 1991, is one of unresolved taxon, which presents major taxonomic difficulties (Shimada *et al.*, 2007). This genus is endemic to Borneo and its species are common frogs around the mountain streams of this island. This genus is not readily distinguishable on the basis of adult morphology from other ranid frogs such as *Hylarana* Tschudi, 1838 (Inger, 1966), but is recognised as distinct because of its unique larval morphology. Tadpoles of *Meristogenys* are specialised for life in strong currents, having a heavy body that is broadly rounded at the snout and flat below. A sizeable oral disk beneath the snout is followed by a large sucker, which covers a larger portion of the abdomen (a “gastromyzophorous” larva; Inger, 1966).

Based on these unique larval features, Inger (1966) moved the type species of this genus, *Rana jerboa* (Günther, 1872) to the genus *Amolops* Cope, 1865. At that time, *Amolops* (sensu lato) included many species locating in wide area of Southeast Asia, including south China. However, Yang (1991) established a genus *Meristogenys* to embrace eight species of Bornean *Amolops*. By contrast, Dubois (1992) considered this taxon as a subgenus of *Amolops*, but distinct generic status of *Meristogenys* is now established by molecular works (e.g. Matsui *et al.*, 2006).

Among the nine species known in this genus, *M. whiteheadi* (Boulenger, 1887) is probably the most controversial one. The taxonomic controversy of this species mainly concerns the lengths of its hind limb. This species was originally described in the genus *Rana* and separated from another Sarawak species, *R. jerboa* on the basis of its shorter hind limb (Boulenger, 1887, 1891); some researchers, however, have challenged this distinction (Mocquard, 1890, 1892; Inger, 1966), and Inger (1966) rejected the validity of *R. whiteheadi*, because he found no critical differences between these two species. Inger & Gritis (1983) reported that the range of tibia length (TL) relative to snout-vent length (SVL) in this species was much smaller than those of other species. Based on this

point, they resurrected *A. whiteheadi* as a valid species.

Taxonomically, this genus is one of the most difficult groups, because the number of known larval forms is greater than that of adults for which species name are given. In order to solve this problem, Shimada *et al*. (2007) studied larval *Meristogenys* collected from a locality in Borneo (Mahua, Crocker Range National Park, Sabah, Malaysia). Among the six genetic lineages (lineages 1–6) they found, lineage 2 had adult characters similar to *M. whiteheadi*, but the TL ratio relative to SVL was much greater than that reported by Inger & Gritis (1983). Thus, they did not determine whether true *M. whiteheadi* was included in their collections. Here, we examined *Meristogenys* specimens from several localities in Sabah and Sarawak using molecular and morphological analysis, and re-evaluated the taxonomic status of this species.

MATERIALS AND METHODS

Following the key of Matsui (1986), 143 adults (115 males and 28 females) and two male juveniles were identified as *M. whiteheadi*: (1) broad web reaching disk of fourth toe; (2) body large, SVL usually greater than 41 mm in males and 66 mm in females; (3) rear of thigh dark brown, dusted with small light spots; (4) short leg, tibia length relative to SVL usually less than 0.70. However, not all specimens strictly fit Matsui's (1986) key. For example, even when a specimen's tibia length exceeded the range that Matsui (1986) had proposed, it was identified as *M. whiteheadi* because it satisfied all other diagnostic characters of this species. We followed the procedure of Shimada *et al*. (2007) to preserve specimens and to determine sex and maturity. Specimens were collected from 14 localities in Sabah and Sarawak [Fig. 1 and Table 1; Kepipiyo, Kimanis, Mahua, Melalap, Ulu Senagang from Crocker Range National Park, Kiau, Melangkap, Monggis, Nalumad, Poring, Wario from Kinabalu Park, Trus Madi and Mendolong, all in Sabah, and Bario in Sarawak]. Of these 143 specimens, tissue samples from 50 specimens (one from Bario, one from Kimanis, 13 from Mahua, one from Poring, three from Ulu Senagang and 31 from Wario) were preserved in ethanol and used for molecular analyses. We collected larval specimens from four of those 14 localities (Bario, Mahua, Ulu Senagang and Wario) plus another locality (Sg. Tinuman) near Kinabalu Park, whose mitochondrial DNA (mtDNA) was similar to that of adult *M. whiteheadi*. We also examined some larval specimens without molecular data as long as they shared morphological characteristics with molecularly identified larvae.

To resolve the phylogenetic relationship among the lineages found in *M. whiteheadi*, we added *M. amoropalamus* (Matsui, 1986), *M. kinabaluensis* (Inger, 1966),

M. jerboa, *M. maryatiae* [“*Meristogenys* sp.” in Shimada *et al.* (2008)], and *M. orphnocnemis* (Matsui, 1986) examined in Shimada *et al*. (2008). As Shimada *et al*. (2008) found two cryptic species in *M. amoropalamus* (lineage 1 and lineage 3-4), we added both of them here. Moreover, we added *M. poecilus* (Inger & Gritis, 1983) from Lanjak Entimau, Sarawak. As hierarchical outgroups, we used a ranid, *Rana nigromaculata* Hallowell, 1861, and a dicroglossid, *Fejervarya limnocharis* (Boie, 1835).

MOLECULAR ANALYSIS

We obtained DNA sequence data from the muscle or liver tissue samples preserved in 99% ethanol. We reconstructed phylogenetic trees from three data sets as given below:
(i) Approximately 950 base pairs (bp) of the partial sequences of 12S rRNA (12S: 440-451 bp) and cytochrome *b* (cytb: 503 bp) from all specimens were examined to clarify the gross genetic structure of *M. whiteheadi*.
(ii) Approximately 5900 bp of mitochondrial 12S, 16S rRNA (16S), NADH dehydrogenase subunit 1, 2 (ND1, 2), tRNAs (valin, leucine, isoleucine, glycine, methionine and tryptophan) and cytb using one or two specimens from each lineage identified as *M. whiteheadi* were examined to resolve the genetic relationships between these lineages and other species. Among these 11 mitochondrial regions, 12S, tRNA tryptophan and cytb were partial sequences, while the others were complete.
(iii) Approximately 3700 bp of the partial sequences of nuclear proopiomelanocortin A (POMC), recombination activating protein 1 (RAG-1), rhodopsin (RH1), solute carrier family 8 member 3 (SLC8A3) and sodium/calcium exchanger 1 (NCX1) from the same specimens as (ii), were examined to compare the phylogenetic information in nuclear DNA (nuDNA) and those in mtDNA. Of these five fragments, RH1 contains an intron, while the others are all exons. Additionally, as Stuart (2008) obtained a RAG-1 sequence of “*M. whiteheadi*” (EF088253) from Mendolong in Sabah, we compared his sequence with ours.

DNA was extracted using standard phenol–chloroform extraction procedures. We used the primers shown in Appendix 1 to amplify and sequence the seven fragments of the mitochondrial and nuclear genomes (12S-tRNA tryptophan, cytb, POMC, RAG-1, RH1, SLC8A3 and NCX1). The polymerase chain reaction (PCR) cycling, precipitation and sequencing procedures were identical to those of Shimada *et al*. (2008). Newly obtained sequences were deposited in GenBank (AB526608–AB526731). We subjected the data to three different methods of phylogenetic reconstruction: (1) the maximum

parsimony (MP) analysis, with transitions and transversions given equal weight; (2) the maximum likelihood (ML) analysis, based on the substitution model and phylogenetic parameters derived from a hierarchical likelihood ratio test (hLRT) in Modeltest 3.06 (Posada & Crandall, 1998); and (3) Bayesian analysis, with the model derived from an hLRT in MrModeltest (Nylander, 2002), with the run using 10000000 generations, sampling a tree every 100 generations and discarding the initial 10000 trees as burn-in. We followed Matsui *et al*. (2006) for the MP and ML heuristic methods. Except for the Bayesian approach, which used MrBayes (Huelsenbeck & Ronquist, 2001), all analyses were conducted with PAUP4.0b (Swofford, 2002). Pairwise comparisons of corrected sequence divergences [Kimura's two-parameter (K2p) distances (Kimura, 1980)] were also calculated using PAUP. The confidential values of MP and ML trees were tested using bootstrap analyses (Felsenstein, 1985) with 2000 replicates for MP and 500 for ML (Hedges, 1992). Following Matsui *et al*. (2006), we considered bootstrap values of more than 70% and posterior probabilities of more than 95% to be statistically significant.

To test certain phylogenetic hypotheses, we applied Templeton tests (Templeton, 1983) with the MP tree and the Shimodaira-Hasegawa test (SH test; Shimodaira & Hasegawa, 1999) using the ML tree. These tests compare the scores of optimal trees under certain restricted and non-restricted optimal trees. If the former was significantly worse than the latter, we rejected the restriction.

MORPHOLOGICAL ANALYSIS OF ADULTS

We measured 20 morphological characters: snout-vent length (SVL); 12 characters on the head [head length (HL), snout-nostril length (S-NL), nostril-eye length (N-EL), snout length (SL), eye length (EL), tympanum-eye length (T-EL), vertical diameter of tympanum (TDv), horizontal diameter of tympanum (TDh), head width (HW), internarial distance (IND), interorbital distance (IOD), upper eyelid width (UEW)]; and seven characters on the limbs [forelimb length (FLL), lower arm and hand length (LAL) from elbow to tip of third finger, hand length (HAL), hind limb length (HLL), thigh length (THIGH), tibia length (TL), and foot length (FL)]. Dial callipers were used to make measurements to 0.1 mm. See Matsui (1984) for detailed definitions of each character. For juveniles, we measured only the SVL. We treated male and female *Meristogenys* separately because the sexes are quite different in body size. For males we had five localities (Kepipiyo, Mahua, Mendolong, Monggis and Wario) with a sufficient number of specimens for statistical analysis. Using specimens collected from all five

localities, we compared SVL using one-way ANOVA with the Tukey-Kramer multiple comparison test (Zar, 1984). We also compared the ratios of each character to the SVL using the Kruskal-Wallis test with Dunn's multiple comparisons test (Zar, 1984). We had a sufficient number of female specimens from only two localities (Mahua and Wario), and used the Student *t*-test (Zar, 1984) to compare the SVL and the Mann-Whitney *U*-test (Zar, 1984) for analysing character ratios.

For the 54 specimens (43 males and 11 females) from Bario, Mahua, Poring, Ulu Senagang and Wario, we additionally compared the relative lengths of the hind limb following Boulenger (1891) to determine whether the tibia-femoral articulation reaches the tympanum when the hind limb is pressed forward along the body.

We also measured the SVL and TL of several other congeneric species—*M. amoropalamus*, *M. jerboa*, *M. kinabaluensis*, *M. orphnocnemis*, *M. phaeomerus* (Inger and Gritis, 1983) and *M. poecilus*—to confirm whether *M. whiteheadi* is truly distinguished from the other species by shorter hind limbs. Of the two cryptic species included in *M. amoropalamus* (Shimada *et al*., 2008), we used lineage 1 here. See Appendix 2 for localities and specimen vouchers.

Colour patterns of the upper lip

Although all adult specimens had dark spots on the lower lip, we found a large variation in the colour pattern of the upper lip. We classified the colour pattern of the upper lip into five types: pattern 1-a = regularly arranged dark spots with a similar size to those on the lower lip; pattern 1-b = irregular dark spots smaller than those on the lower lip; pattern 2 = uniformly black; pattern 3 = uniformly grey; pattern 4 = uniformly white (Fig. 2).

Morphological analysis of tadpoles

To ascertain morphological variation in the larvae, we examined 31 tadpoles determined to be *M. whiteheadi* through mtDNA and/or morphological traits. We followed Shimada *et al*. (2007) in the procedure for preserving larval specimens. We measured 13 characters using a dial callipers to 0.1 mm: (1) total length (TTL), (2) head-body length (HBL), (3) head-body width (HBW), (4) head-body height (HBH), (5) sucker width (SUW), (6) sucker length (SUL, distance between the base of oral disk and posterior end of the sucker), (7) oral disk width (ODW), (8) snout width (SNW), (9) eyeball diameter (ED), (10) eye-snout distance (ESD: distance between the snout and anterior

end of the eyeball, (11) internarial distance (IND: minimum distance between narial openings), (12) interorbital distance (IOD, minimum distance between eyeballs) and (13) tail height (TLH). The tail length (TLL) was calculated by subtracting the HBL from TTL. We followed Shimada *et al*. (2007) for the description of dermal glands, the pattern of surface projections, labial tooth row formulae (LTRF), the status of lower jaw sheaths and the serrations of both jaw sheaths

RESULTS

PHYLOGENETIC ANALYSIS USING SHORT FRAGMENTS OF 12S AND CYTB

We obtained 957 bp of concatenated fragments of 12S and cytb gene for 76 samples including outgroups. Of the 957 characters, 366 were variable and 260 were parsimony-informative. We found 17 haplotypes among 65 total sequences of *M. whiteheadi*, which diverged in sequence from 0.2% to 11.7% (Kimura's two-parameter distance; Kimura, 1980) in 12S and 0.2% to 18.0% in cytb. We estimated the phylogenetic relationships among these haplotypes. MP searches recovered the eight most parsimonious trees of 899 steps [constancy index (CI) = 0.561, retention index (RI) = 0.883]. The best substitution model derived from hLRT was Tamura & Nei's evolutionary model (TrN + G + I; Tamura & Nei, 1993) and general time-reversible (GTR + G + I; Rodriguez *et al*., 1990) evolutionary models for ML and Bayesian inferences, respectively. The likelihood values of the ML and Bayesian trees were –lnL = 5142.86 and 5136.91, respectively. The results of three phylogenetic inferences were slightly different, but the nodes that were significantly supported were completely shared. We therefore show only the Bayesian tree in Fig. 3. In these analyses, all samples of *Meristogenys* formed a monophyletic group (100%, 98% and 95% support in Bayesian posterior probability, ML bootstrap, and MP bootstrap values, respectively). The basalmost placement of *M. kinabaluensis* was recovered in all analysis, but the support values were weak (88%, 70% and 70%). In the *M. jerboa* species group used in this study (*M. amoropalamus*, *M. jerboa*, *M. maryatiae*, *M. orphnocnemis*, *M. poecilus*, and *M. whiteheadi*), we recognised eight lineages, but their phylogenetic relationships remained unclear. Among these eight, three lineages were composed of *M. whiteheadi* as shown below.

(i) Adults and larvae of *M. whiteheadi* from Mahua formed a monophyletic group (all 100% support) with few genetic variations (0.2% in 12S and 0.2% in cytb).

(ii) Adults and larvae of *M. whiteheadi* from Kimanis, Ulu Senagang and Sg. Tinuman formed a monophyletic group (all 100% support) with few genetic variations (0.7% in 12S and 1.8% in cytb).
(iii) Adults and larvae of *M. whiteheadi* from Bario, Poring and Wario formed a monophyletic group (100%, 99% and 99% support). In this clade, specimens from Wario and Poring formed a monophyletic group (all 100% support) with few genetic variations (0.5% in 12S and 1.2% in cytb); specimens from Bario formed a sister clade with relatively large genetic distances (2.3%–2.8% in 12S and 6.8%–7.0% in cytb).

These results support the presence of three allopatric lineages in *M. whiteheadi*. We name them here as the Mahua, Ulu Senagang and Wario lineages.

PHYLOGENETIC ANALYSIS USING LONG FRAGMENTS OF MTDNA

To resolve the evolutionary relationships among the three lineages currently identified as *M. whiteheadi*, we chose a single specimen from the Mahua, Ulu Senagang lineages and two specimens from the Wario lineage (from Bario and Wario), and reconstructed phylogenetic trees of *Meristogenys* using the relatively long fragments of concatenated mtDNA.

We obtained 5993 bp of mtDNA, of which 2335 were variable and 1457 were parsimony informative. The numbers of the aligned length, variable sites and parsimony informative sites of each region are shown in Table 2. The MP search recovered a most parsimonious tree of 5760 steps (CI = 0.577, RI = 0.351). The best substitution model derived from hLRT was the GTR + G + I evolutionary model (Rodriguez *et al*., 1990) for both the ML and Bayesian inferences. The likelihood values of the ML and Bayesian trees were identical: –lnL = 31041.16. The results from three phylogenetic inferences were slightly different, but the nodes that were significantly supported were completely identical (Fig. 4 left; only the Bayesian tree is shown). Compared to the trees derived from shorter sequences, the supporting values increased at many nodes and the following relationships were indicated by the three analyses as statistically reliable:
(iv) monophyly of *Meristogenys* species against outgroups (all 100% support).
(v) monophyly of *Meristogenys* species other than *M. kinabaluensis* (the *M. jerboa* species complex: 100%, 97% and 100% support).
(vi) monophyly of *M. maryatiae*, *M. orphnocnemis*, *M. poecilus*, lineages 3 and 4 of *M. amoropalamus*, the Mahua and Wario lineages of *M. whiteheadi* (100%, 92% and 72% support).
(vii) monophyly of *M. orphnocnemis* and lineage 3 and 4 of *M. amoropalamus* (100%,

100% and 96% support).
(viii) monophyly of lineages 3 and 4 of *M. amoropalamus* (all 100% support).
(ix) monophyly of specimens from Bario and Wario of the Wario lineage of *M. whiteheadi* (all 100% support).

In contrast, the following relationships were supported only by one or two analyses of the Bayesian, ML or MP analysis:
(x) monophyly of the *M. jerboa* species complex other than *M. jerboa* (86%, 70% and <50% support).
(xi) monophyly of the *M. jerboa* species complex other than *M. jerboa* and the Ulu Senagang lineage of *M. whiteheadi* (95%, 61% and <50% support).
(xii) monophyly of *M. maryatiae*, *M. orphnocnemis* and lineages 3 and 4 of *M. amoropalamus* (100%, 98% and 62% support).

In these phylogenetic trees, the monophylies of the Ulu Senagang lineage and other two lineages were clearly rejected [(vi) and (xi)]. The monophyly of the Mahua and Wario lineages was not supported in high support values. The genetic distances among these lineages were relatively large (more than 5% in 12S and 13% in cytb; see "Taxonomic relationships" in Discussion).

Both the Templeton and SH tests clearly rejected the three hypothesis of the monophyly of *M. whiteheadi*: (1) monophyly of the Mahua, Ulu Senagang and Wario lineages, (2) monophyly of the Ulu Senagang and Wario lineages and (3) monophyly of the Mahua and Ulu Senagang lineages. However, monophyly of the Mahua and Wario lineages was not significantly rejected (Table 3).

PHYLOGENETIC ANALYSES USING NUDNA

To confirm the results from mtDNA, we reconstructed the phylogenetic trees of *Meristogenys* using nuDNA. We obtained 3736 bp of nuDNA, of which 454 were variable and 115 were parsimony informative. The numbers of the aligned length, variable sites and parsimony-informative sites of each region are shown in Table 2. The MP search recovered 14 most parsimonious trees of 525 steps (CI = 0.895, RI = 0.703). The best substitution model derived from hLRT was TrN + G (Tamura & Nei, 1993) and GTR + G (Rodriguez *et al*., 1990) evolutionary models for the ML and Bayesian inferences, respectively. The likelihood values of the ML and Bayesian trees were –lnL = 8101.67 and 8093.94, respectively. The results from three phylogenetic inferences were slightly different, but the nodes with significant support were completely identical (Fig. 4 right; only the Bayesian tree is shown). The following relationships were

supported by results of the three analyses:
(xiii) monophyly of *Meristogenys* species against outgroups (all 100% support).
(xiv) monophyly of *Meristogenys* species other than *M. kinabaluensis* (the *M. jerboa* species complex: all 100% support).
(xv) monophyly of *M. orphnocnemis*, *Meristogenys maryatiae*, lineages 3 and 4 of *M. amoropalamus* (100%, 79% and 83% support).
(xvi) monophyly of *M. maryatiae* and *M. orphnocnemis* (100%, 79% and 83% support).
(xvii) monophyly of lineages 3 and 4 of *M. amoropalamus* (completely identical sequences; all 100% support).
(xviii) monophyly of specimens from Bario and Wario in the Wario lineage of *M. whiteheadi* (all 100% support).

In contrast, the following relationship was supported only by the Bayesian analysis:
(xix) monophyly of the Wario lineage of *M. whiteheadi*, lineages 3 and 4 of *M. amoropalamus*, *M. maryatiae*, and *M. orphnocnemis* (100%, 69% and 67% support).

The phylogenetic trees based on mtDNA and nuDNA differed at some highly supported nodes [(vi) and (xix), (vii) and (xvi)]. However, they agree that *M. whiteheadi* is divided into three distinct lineages and does not constitute a monophyletic group.

The RAG-1 sequence of "*M. whiteheadi*" (EF088253) collected from Mendolong and reported by Stuart (2008) did not differ from our Ulu Senagang lineage; however, it did differ in nine, 13 and 12 sites of 783 sites in *M. whiteheadi* from Mahua, Bario and Wario, respectively.

MORPHOLOGICAL ANALYSES OF ADULTS

Measurement data for 20 characters in 14 populations of *M. whiteheadi* are shown in Fig. 5 and Table 4. For males, populations were assigned either to the large type ($\geq$50 mm) or the small type (<50 mm). Most of male specimens from Kepipiyo, Mendolong, Melalap and Ulu Senagang showed SVLs >50 mm, while those from Kiau, Mahua, Melangkap, Monggis, Nalumad, Trus Madi and Wario had SVLs <50 mm. Although we could not collect any adult males from Kimanis, we regarded this site as having the large type because we collected an immature male with a SVL of 47.7 mm there. From Bario and Poring we collected two and one male specimens with a SVL of around 50 mm, respectively, but could not assign these specimens to either type on the basis of their body size. In contrast to males, we could find no clear tendencies in the body size of females. Comparisons of localities with sufficient numbers of specimens resulted in

significant differences in male SVL (ANOVA, $P < 0.05$), but not in female SVL (Student's *t*-test, $P > 0.05$). A Tukey-Kramer test showed males from Mendolong and Kepipiyo to be larger than those from Mahua, Monggis and Wario. The Mendolong samples were shown to be larger than those from Kepipiyo; of the latter three locales, the Mahua samples were larger than the Wario samples.

The Kruskal-Wallis tests indicated significant heterogeneities in males from the various localities in 14 characters: HL, HW, EL, TDh, TDv, SL, IOD, UEW, FLL, LAL, HAL, HLL, TL and FL. Dunn's multiple comparisons showed that males from Mahua had significantly larger IODs than other males: Ma > Mo, Ma > Wa, Ma > Ke, Ma > Me (Mo = Monggis, Wa = Wario, Ma =Mahua, Ke = Kepipiyo, Me = Mendolong), and males from Kepipiyo and Mendolong had significantly smaller heads than those from elsewhere: Mo > Me in HW, EL and UEW; Wa > Me in HL, HW, EL, TDh and TDv; Ma > Me in HW, TDh, TDv and IOD; Mo > Ke in UEW; Wa > Ke in HL, TDh and TDv; and Ma > Ke in TDh, TDv and IOD). Additionally, males from Mahua had longer limbs than other males: Ma > Me in LAL, HAL, FL, HLL, and TL; Ma > Wa in HLL and TL; Ma > Ke in LAL). Apart from these tendencies, only one combination (Mo > Ma in UEW) was significantly different in males.

In females we could compare only the populations from Mahua and Wario. *U*-tests showed significant heterogeneity between them in five characters: N-EL, HAL, HLL, THIGH and FL. Dunn's multiple comparisons agreed with the results for males in the longer limbs of Mahua specimens (Ma > Wa in HAL, HLL, THIGH and FL). Apart from this tendency, only one relationship (Wa > Ma in N-EL) was significant in females.

In all 43 males examined (one from Bario, nine from Mahua, one from Poring, one from Ulu Senagang, and 31 from Wario), the tibia-femoral joint reached the tympanum when the hind limb was pressed forward. This joint did not reach the tympanum in 11 females (one from Bario, four from Mahua, one from Ulu Senagang and five from Wario).

The TL/SVL ratio in male *M. whiteheadi* ranged from 65.1% to 77.4% (median = 70.5%) and showed geographic variations (Table 4). The TL/SVL ranged from 68.5% to 74.4% (median = 71.2%) in *M. amoropalamus* (lineage 1), 67.8% to 74.4% (72.0%) in *M. jerboa*, 64.7% to 69.4% (67.6%) in *M. kinabaluensis*, 65.4% to 73.7% (69.0%) in *M. orphnocnemis*, 67.4% to 74.4% (70.7%) in *M. phaeomerus* and 69.6% to 77.8% (73.5%) in *M. poecilus* (Fig. 6).

COLOUR PATTERNS OF THE UPPER LIPS

Most samples from Mahua and Trus Madi had the 1-a colour pattern of the upper lip, although a few samples were classified as pattern 1-b (Table 5). Most samples from other localities had pattern 2, 3 or 4 except for two specimens from Bario and Wario with 1-b. No different tendencies appeared to exist between male and female specimens.

MORPHOLOGICAL ANALYSES OF LARVAE

Fifteen larvae from five localities (Bario, Mahua, Sg. Tinuman, Ulu Senagang and Wario) were examined. Larvae from Bario, Mahua, Ulu Senagang and Wario had the same DNA sequences as those of sympatric adults. Although we had no adult specimens from Sg. Tinuman, the larvae from there had sequences similar to those of Ulu Senagang adults. From the five localities, we chose the other 29 larvae morphologically similar to these molecularly assigned larvae, and examined the morphology of a total of 44 larval specimens. Specimen numbers, developmental stages (Gosner, 1960) and detailed data for each character are shown in Tables 6 and 7.

At stages 26-29, larvae from Ulu Senagang and Sg. Tinuman had approximately the same body size (HBL more than 13 mm; Table 7) and seem to be larger than those from Bario, Mahua and Wario (HBL less than 12 mm), although small sample size compared yielded only Ulu Senagang sample to be larger than Bario sample in Dunn's multiple comparison test. In LTRF, the specimens from Mahua and Wario had fewer rows [7(4–7)/6(1)] than those from Sg. Tinuman and Ulu Senagang [7(4–7)/7(1) and 7(4–7)/8(1), respectively] at the same developmental stages. Larvae from Bario were intermediate between them with LTRFs of both 7(4–7)/6(1) and 7(4–7)/7(1). All larvae had divided upper jaw sheaths and an undivided lower jaw sheath. The larvae from Bario, Mahua and Wario had fewer serrations than those from Sg. Tinuman and Ulu Senagang at the same developmental stages (the serrations of an upper jaw sheath of stages 26–29: Bario = 6–7, Mahua = 6–7, Wario = 5–7, Sg. Tinuman = 10–11, Ulu Senagang = 8–10). All larvae had surface projections at least on part of their bodies. All larvae had postorbital, infraorbital, prespiracular and midlateral glands, except for some specimens from Sg. Tinuman, but no larvae had ventral glands. No larvae had glands on their dorsal fin, but some had ventral fin glands. Most specimens from Bario, Mahua and Wario had more than six ventral fin glands, while larvae from Sg. Tinuman and Ulu Senagang had none, or at most 1–2 glands; a larva from Ulu Senagang, however, had six glands.

SYSTEMATICS

Meristogenys stigmachilus sp. nov. (Fig. 7A, B)

Meristogenys cf. *whiteheadi*: Shimada et al., 2007, p. 187, fig 4B

Diagnosis

A large species of the *M. jerboa* species group (Matsui, 1986), with male SVL 43.3-50.0 mm, female SVL 69.2-79.6; rear of thigh dark brown, dusted with small irregular light spots; fourth toe fully webbed to disk, with narrow fringes on both sides to disk in males, while broad web to disk in females; length of tibia relative to SVL usually greater than 0.72; dark spots present both on upper and lower lips.

Etymology

Specific name from *stigmas* (Gr.), meaning spot or tattoo, and *chilus* (Gr.) meaning lips, referring to the spotted upper lips of this species.

Holotype

Sabah Parks (SP) 20350; an adult male from Mahua station, Crocker Range National Park, Sabah, Malaysia (5°48’00’’ N, 116°24’05’’E, alt 1200 m a.s.l.), collected by staff of Zoological Unit of Sabah Parks on 27 August 2003.

Paratypes

Two males and a female from the type locality: SP 2466 and 2478, University Malaysia Sabah (BORNEENSIS) 12434.

Referred specimens

Ten males and seven females from the type locality and Mt. Trus Madi (Sg. Rompon and Sg. Pergas; See Appendix 2)

Description of holotype (measurements in mm)

Body moderately stout, SVL 44.1; head subtriangular, longer (18.3) than wide (16.0); snout somewhat blunt, projecting slightly beyond lower jaw; eyes elevated; canthi sharp, slightly concave; lores slightly oblique, concave; nostrils lateral, just below canthal edge, distinctly closer to tip of snout (3.2) than to eye (3.5); IND (5.2) wider than IOD (4.3);

latter narrower than UEW (4.6); SL 7.0; eye-mouth distance 1.5; nostril-mouth distance 2.7; pineal spot visible, slightly behind the line connecting anterior corners of orbits; tympanum distinct, TDv (4.3) and TDh (4.0) less than two-thirds of EL (7.1); T-EL (1.6) two-fifth of TDv and TDh; nostril-tympanum distance 11.3; snout-tympanum distance 15.0; vomerine teeth obvious, in small oblique groups separated by the half of one group, groups on line connecting rear rims of choanae; tongue deeply notched, without papilla; paired subgular vocal sacs form gular pouches at corners of throat; vocal opening just inside commissures of jaws.

Fingers slender, first (6.0) and second subequal, much shorter than third (10.1); tips expanded into disks having circummarginal grooves; the disk of first finger smallest of all; disks of second, third (diameter 1.6) and fourth fingers subequal, two-fifths of TDv and TDh; no fringes of skin along fingers; no supernumerary metacarpal tubercles; distinct nuptial pads covering dorsal and medial surfaces of the first finger from its base to subarticular tubercle.

Hindlimb (99.3) approximately 3.3 times FLL (30.5); LAL 24.7; HAL 14.5; tibia long (33.4); heels overlapping when limbs are held at right angles to body; THIGH (28.2) and FL (26.8) much shorter than TL. Toe disks similar to those of fingers in shape and size (disk diameter of fourth toe 1.4); all toes fully webbed to disks, fourth toe with narrow fringes on both sides to disk; excision of web between fourth and fifth toes reaching to the level of proximal end of middle subarticular tubercle of fourth toe; a narrow fringe of skin along medial edge of first toe; inner metatarsal tubercle elliptical, shorter (1.9) than distance between it and subarticular tubercle of first toe; a small round, raised outer metatarsal tubercle.

Skin of dorsum finely granular on head and trunk; a weak fold from above eye to axilla; a low dorsolateral glandular fold; side of trunk coarsely granular; thighs strongly rugose above; throat smooth; chest and abdomen weakly rugose.

Colour in life (See Fig. 2A, 2B, and 7A)

Dorsum light brown dotted with dark brown; lores with interrupted dark streaks below canthus; upper and lower lips whitish yellow with small obvious dark spots; iris bicoloured, pale yellowish green above and pale brown below with a small portion of reddish orange in between; a small light circle on the centre of a tympanum; a blackish brown band beginning behind eye bordering rear of the tympanum, diverging above the tympanum and nearly reaching the inguinal area; dorsal and ventral boundaries obscure; limbs marked dorsally with alternating light and dark brown crossbars; a short dark streak ventrally at insertion of arm; rear of thigh light brown with scattered light dots;

throat and chest whitish with dots of melanophores; abdomen whitish; ventral surfaces of legs whitish with dense dots of melanophores.

Colour in alcohol

Colour pattern has not been changed even after preservation in ethanol for several years, except for iris colour which has disappeared soon after the fixation in formalin solution.

Larvae (Fig. 7B)

We examined three specimens of stage 26-27 of Gosner (1960) from Mahua. These specimens are identical to those used by Shimada et al. (2007) to define their larval morphotype 2. Head-body length ranges from 9.5-11.5 mm (Table 7).

Head-body oval, broadly rounded at snout, flat below; eyes dorsolateral, not visible from below, pointing outward; nostril open, rim not raised, closer to eye than to tip of snout.

Oral disk ventral; upper lip separated from snout by a groove; upper lip with short marginal papillae in lateral third, inframarginal papillae near corner; lower lip with uninterrupted row of short marginal papillae; labial tooth row formulae 7(4-7)/6(1); upper jaw sheaths M-shaped, lower V-shaped; upper jaw sheaths divided; lower jaw sheaths undivided; jaw sheaths heavy, completely black except for outer margins that are covered by thin film; upper sheath film thicker than the lower; outer surface of lower jaw sheaths with several weak ribs; margin finely serrate, 6-7 and 6 serrae on a half of upper and lower jaw sheaths, respectively; a large suctorial abdominal disk following oral disk; peripheral part of disk darkened and keratinized.

Spiracle sinistral; tube moderately long, length subequal to length of eyeball, pointing upward and backward, free of body wall for half its length; anal tube median, free of tail; tail heavily muscled, dorsal margin strongly convex, deepest before middle, tapering to slightly pointed tip; caudal muscle deeper than fins in basal half; dorsal fin origin behind body, fin deeper than ventral fin except in final fourth; ventral fin origin at end of proximal third of tail; head-body with four pairs of glandular clusters; a postorbital cluster about an eye length behind eye, with 3-4 glands; a infraorbital at the base of snout, with 3-6 glands; a prespiracular cluster just anterior to spiracle, with 3-7 glands; a midlateral at the posterior end of body, with 2-5 glands; no dorsal fin glands; 1-14 ventral fin glands; head-body scattered dorsally with minute protuberances anterior to eye in older larvae; lateral line pores indistinct.

Head-body light brown dorsally and laterally, sometimes posterior half of lateral surface dark brown; caudal muscle light brown; fins translucent with scattered

pigmentations.

Range

This species has been collected from the type locality (Mahua; alt. 1063 m a.s.l.) and Mt. Trus Madi (850 m). Probably this species is distributed on relatively high areas of the Crocker Range, Western Sabah, Malaysia.

Natural History

Gravid females and larvae were collected from Mahua in August 2003; neither was collected during the surveys at the same area in December 2003, March and August 2005, or March 2006. However, judging from other congeneric species (Inger & Bacon, 1968), this species might also breed all around the year. At the type locality, larvae were collected from a river at the width of 3-5 m, but we are not certain if this environment is the typical larval habitat of this species because the density of larvae was quite low.

Variation

Males and females differ greatly in SVL (male: 43.3-50.0 mm; female: 69.2-79.6 mm) and relative ratio of TDh and TDv to SVL (male: 9.3-11.4 % in TDv, 8.6-11.1% in TDh; female: 6.4-7.5 % in TDv, 5.8-6.8 % in TDh; see Table 4). Dorsal colouration changes from dark brown to light brown depending on surrounding environment. Usually a captive individual in the daytime has colouration lighter than it was when collected in the night.

Meristogenys stenocephalus sp. nov.

Meristogenys whiteheadi: Stuart, 2008, p. 51.

Diagnosis

A large species of the *M. jerboa* species group (Matsui, 1986), with male SVL 48.0-60.4 mm and female SVL 76.5-86.6 mm; rear of thigh dark brown, dusted with small irregular light spots; fourth toe fully webbed to disk; TL relative to SVL usually greater than 0.70; head narrow, HW and HL relative to SVL usually less than 0.35, and 0.41, respectively.

Etymology

Specific name from *stenos* (Gr.), meaning narrow, and *cephalus* (Gr.) meaning heads, referring to the relatively small and narrow head of this species.

Holotype

BORNEENSIS 12810; an adult male from Ulu Senagang, Crocker Range National Park, Sabah, Malaysia (5°20'40'' N, 116°01'45''E, alt 550 m a.s.l.), collected by Masafumi Matsui, Kanto Nishikawa, Tomohiko Shimada and Ahmad Sudin on 18th August 2003.

Paratypes

BORNEENSIS 12809; a female from the type locality.

Referred specimens

29 males, three females, and two juveniles from Kimanis, Melalap, Kepipiyo, and Mendolong, all from Sabah (See Appendix 2).

Description of holotype (measurements in mm)

Body moderately slender, SVL 60.4; head triangular, longer (24.3) than wide (19.5); snout obtusely pointed, projecting slightly beyond lower jaw; eyes elevated; canthi sharp, slightly concave; lores slightly oblique, concave; nostrils lateral, just below canthal edge, distinctly closer to tip of snout (4.3) than to eye (5.3); IND (6.1) wider than IOD (5.1); latter narrower than UEW (6.6); SL 10.1; eye-mouth distance 1.8; nostril-mouth distance 3.3; pineal spot visible, slightly behind the line connecting anterior corners of orbits; tympanum distinct, TDv (5.2) and TDh (5.0) less than two-thirds of EL (9.1); T-EL (2.1) two-fifths of TDv and TDh; nostril-tympanum distance 15.6; snout-tympanum distance 20.4; vomerine teeth obvious, in small oblique groups separated by the half of one group, groups on line connecting rear rims of choanae; tongue deeply notched, without papilla; paired subgular vocal sacs forming gular pouches at corners of throat; vocal opening just inside commissures of jaws.

Fingers slender, first (8.2) and second subequal, much shorter than third (12.4); tips expanded into disks having circummarginal grooves; the disk of first finger smallest of all; disks of second, third (2.4) and fourth fingers subequal in diameter, half of TDv and TDh; no fringes of skin along fingers; no supernumerary metacarpal tubercles; distinct nuptial pads covering dorsal and medial surfaces of the first finger from its base to subarticular tubercle.

Hindlimb (127.3) approximately 3.2 times length of FLL (39.4); LAL 31.2; HAL 18.1; tibia long (43.3); heels overlapping when limbs are held at right angles to body;

THIGH (36.8) and FL (33.7) much shorter than TL. Toe disks similar to those of fingers in shape and size (disk diameter of fourth toe 2.4); all toes fully webbed to disks; excision of web between fourth and fifth toes reaching to middle of proximal and middle subarticular tubercle of fourth toe; a narrow fringe of skin along medial edge of first toe; inner metatarsal tubercle elliptical, shorter (2.9) than distance between it and subarticular tubercle of first toe; a small round, raised outer metatarsal tubercle.

Skin of dorsum finely granular on head and trunk; a weak fold from above eye to axilla; a low dorsolateral glandular fold; side of trunk coarsely granular; thighs strongly rugose above; throat smooth; chest and abdomen weakly rugose.

Colour in life (See Fig. 2E and 7C)

Dorsum light to dark brown without markings; supratympanic fold with interrupted dark streak; upper lip whitish yellow without markings; lower lip whitish with weak dark spots; iris bicoloured, yellowish green above and below with a small portion of reddish orange in between; centre of tympanum dark without light spot; a blackish brown band beginning behind eye bordering rear of the tympanum, diverging above the tympanum and nearly reaching the inguinal area; dorsal and ventral boundaries obscure; limbs marked dorsally with alternating light and dark brown crossbars; rear of thigh light brown with scattered light spots; throat, chest, and abdomen whitish; ventral surfaces of legs whitish with dense dots of melanophores.

Colour in alcohol

Colour pattern has not been changed after preservation in ethanol for several years, except for iris colour which soon disappeared after the fixation in formalin solution.

Larvae (Fig. 7D)

We examined 26 specimens of stage 26-40 of Gosner (1960) from Sg. Tinuman and Ulu Senagang. Head-body length ranges from 12.6-14.9 mm in St. 26-29, 16.4-18.9 mm in St. 30-33, 19.0-22.1 mm in St. 34-37, and 21.2-24.4 mm in St. 38-40 (Table 7)

Head-body oval, broadly rounded at snout, flat below, eyes dorsolateral, not visible from below, pointing outward; nostril open, rim not raised, closer to eye than to tip of snout.

Oral disk ventral; upper lip separated from snout by a groove; upper lip with short marginal papillae in lateral third, inframarginal papillae near corner; lower lip with uninterrupted row of short marginal papillae; labial tooth row formulae 7(4-7)/7(1) to 7(4-7)/8(1); upper jaw sheaths M-shaped, lower V-shaped; upper jaw sheaths divided;

lower jaw sheaths undivided; jaw sheaths heavy, completely black except for outer margins covered by thin film; upper sheath film thicker than the lower; outer surface of lower jaw sheaths with several weak ribs; margin finely serrate, 8-19 and 7-13 serrae on a half of upper and lower jaw sheaths, respectively; a large suctorial abdominal disk following oral disk; peripheral part of disk darkened and keratinized.

Spiracle sinistral; tube moderately long, length subequal to length of eyeball, pointing upward and backward, free of body wall for half its length; anal tube median, free of tail; tail heavily muscled, dorsal margin strongly convex, deepest before middle, tapering to slightly pointed tip; caudal muscle deeper than fins in basal half; dorsal fin origin behind body, fin deeper than ventral fin except in final fourth; ventral fin origin at end of proximal third of tail; head-body with four pairs of glandular clusters; a postorbital cluster about an eye length behind eye, with 1-6 glands; a infraorbital at the base of snout, with 0-3 glands; a prespiracular cluster just anterior to spiracle, with 0-9 glands; a midlateral at the posterior end of body, with 0-6 glands; no dorsal fin glands; 0-6 ventral fin glands; whole head-body scattered dorsally with minute protuberances in older larvae; the area occupied by spinules and their density larger in older larvae than those in younger larvae; lateral line pores indistinct.

Head-body light brown dorsally and laterally, sometimes posterior half of lateral surface dark brown; caudal muscle light brown; fins translucent with scattered pigmentations; pigmentations densely covering both fins in older larvae.

Range

Besides the type locality (Ulu Senagang; alt. 550 m a.s.l.), this species has been collected from Kimanis (820 m), Kepipiyo (380 m), Melalap (700 m), Mendolong (590 m), and Sg. Tinuman (750 m). The larvae collected from the Kaingeran River (a part of larva D in Inger, 1966 and Inger and Gritis, 1983) also seem to be this species (See Comparison to known larvae). This species is most likely distributed in hilly areas of the Crocker Range, Western Sabah, Malaysia.

Natural History

Larvae collected in August 2003 and November 2006 at Ulu Senagang and in March 2007 at Sg. Tinuman, showed a wide range of developmental stages. Thus, there seems to be no particular reproductive seasons. Larvae were collected from rivers with a width of 10-15 m in both localities.

Variation

Males and females differ greatly in SVL (male: 48.0-60.4 mm; female: 76.5-86.6 mm) and relative ratio of TDh and TDv to SVL (male: 8.0-10.1 % in TDh, 6.6-9.6 % in TDv; female: 6.3-6.9 % in TDh, 5.5-5.8 % in TDv; see Table 4). The iris of specimens from Ulu Senagang was bicoloured as shown above, while those from Kimanis was bicoloured with yellow above and reddish orange below. We have no information for iris colouration of specimens from other localities. Dorsal colouration changes from dark brown to light brown depending on surrounding environment.

Meristogenys whiteheadi (Boulenger, 1887)

Specimens examined
74 males and 19 females from Kiau, Melangkap, Monggis, Nalumad, Poring, Wario (western Sabah), and Bario (northern Sarawak; See Appendix 2)

Colour in life (See Fig. 2C, 2D, and 7E)
Dorsum light brown to greenish dark brown; lores with interrupted dark streaks below canthus; upper and lower lips dark grey to black; iris bicoloured, whitish brown above and below, with tips of reddish orange in between; a small light circle usually on the centre of a tympanum; a blackish brown band beginning behind eye bordering rear of the tympanum, diverging above the tympanum and nearly reaching the inguinal area; dorsal and ventral boundaries obscure; limbs marked dorsally with alternating light and dark brown crossbars; a short dark streak ventrally at insertion of arm; rear of thigh light brown with scattered light dots; throat and chest whitish with dots of melanophores; abdomen whitish; ventral surfaces of legs whitish with patches of pigmentation of melanophores.

Larvae (Fig. 7F)
We examined 15 specimens of stage 26-29 of Gosner (1960) from Bario and Wario, with head-body length ranging from 8.2-11.8 mm in St. 26-29, 12.5 mm in St. 30, and 15.2 mm in St. 35 (Table 7).

Head-body oval, broadly rounded at snout, flat below, eyes dorsolateral, not visible from below, pointing outward; nostril open, rim not raised, closer to eye than to tip of snout.

Oral disk ventral; upper lip separated from snout by a groove; upper lip with short marginal papillae in lateral third, inframarginal papillae near corner; lower lip with

uninterrupted row of short marginal papillae; labial tooth row formulae 7(4-7)/6(1) in all five specimens from Wario and one specimen from Bario, and 7(4-7)/7(1) in nine specimens from Bario; upper jaw sheaths M-shaped, lower V-shaped; upper jaw sheaths divided; lower jaw sheaths undivided; jaw sheaths heavy and completely black except for outer margins covered by thin film; upper sheath film thicker than the lower; outer surface of lower jaw sheaths with several weak ribs; margin finely serrate, 5-7 and 5-6 serrae on a half of upper and lower jaw sheaths, respectively; a large suctorial abdominal disk following oral disk; peripheral part of disk darkened and keratinized.

Spiracle sinistral; tube moderately long, length subequal to length of eyeball, pointing upward and backward, free of body wall for half its length; anal tube median, free of tail; tail heavily muscled, dorsal margin strongly convex, deepest before middle, tapering to slightly pointed tip; caudal muscle deeper than fins in basal half; dorsal fin origin behind body, fin deeper than ventral fin except in final fourth; ventral fin origin at end of proximal third of tail; head-body with four pairs of glandular clusters; a postorbital cluster about an eye length behind eye, with 1-3 glands; a infraorbital at the base of snout, with 1-5 glands; a prespiracular cluster just anterior to spiracle, with 1-9 glands; a midlateral at the posterior end of body, with 1-9 glands; no ventral and dorsal fin glands; 0-10 ventral fin glands; head-body scattered dorsally with minute protuberances in developed larvae; lateral line pores indistinct.

Head-body light brown dorsally and laterally, sometimes posterior half of lateral surface dark brown; caudal muscle light brown; fins translucent with scattered pigmentations.

Range

In Sabah, this species has been collected around Mt. Kinabalu: Kiau (alt. 900 m a.s.l.), Melangkap (310 m), Monggis (300 m), Nalumad (450 m), Poring (500 m), and Wario (950 m). The larvae collected from Mamut (larva E in Inger, 1966, 1985, Inger & Gritis, 1983) also seem to be this species (See Comparison to known larvae). In Sarawak, *M. whiteheadi* was collected from Bario (1000 m), which is 250 km remote from Mt. Kinabalu. There seems to be disjunction of distribution between these two areas.

COMPARISONS

Meristogenys stigmachilus and *M. stenocephalus* have relatively large SVLs (45–50 and 50–60 mm, respectively, in males and >70 mm in females of both species) and are

easily distinguished from some congeners with small SVLs: *M. amoropalamus*, *M. jerboa*, *M. macrophthalmus*, *M. maryatiae*, *M. orphnocnemis* and *M. phaeomerus* (<41 mm in males and <66 mm in females; Matsui, 1986). *Meristogenys kinabaluensis*, *M. poecilus*, and *M. whiteheadi* are similar to *M. stigmachilus* and *M. stenocephalus* in having large SVLs (>41 mm in males and >66 mm in females). Of these, *M. kinabaluensis* usually lacks outer metatarsal tubercles and has a yellowish-green to moss-green pattern at least on part of the dorsal surface; *M. stenocephalus* and *M. stigmachilus* usually have outer metatarsal tubercles and lack a green pattern on the back. Additionally, males of *M. kinabaluensis* (>65 mm) are larger than males of *M. stenocephalus* and *M. stigmachilus*. *Meristogenys poecilus* is differentiated from *M. stenocephalus* and *M. stigmachilus* by its blotched pattern on the rear of the thigh (a dotted pattern in the latter two species). *Meristogenys whiteheadi* differs from *M. stigmachilus* in the absence of both dark spots on the upper lip and dots on the back; *M. stigmachilus* is characterised by the presence of these markings). *Meristogenys whiteheadi* differs from *M. stenocephalus* in the relatively small male SVL (40–50 mm) and broader head (HW/SVL usually more than 0.35 in *M. whiteheadi* and less than in *M. stenocephalus*). *Meristogenys stigmachilus* and *M. stenocephalus* differ in male body size and colour pattern. The dark spots on the upper lip and dark dots on the back seen in *M. stigmachilus* are absent in *M. stenocephalus*.

The larvae of *M. stigmachilus* and *M. stenocephalus* share morphological characteristics with those of *M. whiteheadi* in having surface projections, undivided lower jaw sheaths, four divided labial tooth rows on the upper jaw and no glands on their dorsal fin or ventral surface. The larvae of *M. stenocephalus*, however, have larger body size, more serrations in the upper jaw sheaths and fewer glands on the ventral fin than larval *M. stigmachilus* and *M. whiteheadi* (see above). Larval *M. stenocephalus* is one of the largest among *Meristogenys* species, judging from previous studies (e.g. Inger, 1966, 1985; Inger & Gritis, 1983; Shimada *et al*., 2007). Head-body lengths in larval stages 26–29 of *M. stigmachilus* and *M. whiteheadi* are less than 12 mm, while those of *M. stenocephalus* are more than 12 mm. No morphological characters exist to distinguish between larval *M. whiteheadi* and *M. stigmachilus*.

COMPARISON TO KNOWN LARVAE

Amolops larva D in Inger & Gritis (1983) (= "*Amolops kinabaluensis*" of Inger, 1985) may include several species, but at least one series among them (FMNH 109492, collected from the Kaingeran River near Tambunan) shares morphological characters

with *M. stenocephalus*, such as labial tooth row formula, serrations of jaw sheaths, sharp surface projections on the head and body and a large body size. This assignment is geographically reasonable because the Kaingeran River is close to Kimanis where we collected *M. stenocephalus*.

Shimada *et al*. (2007) reported that *Amolops* larva E of Inger & Gritis (1983) (= *Amolops* sp. E in Inger, 1985) shares morphological characters with larval morphotype 2 of Shimada *et al*. (2007), which is described here as *M. stigmachilus* sp. nov. However, since we cannot distinguish *M. stigmachilus* and *M. whiteheadi* through larval morphology, we are uncertain as to which name should be assigned to larva E. Yet considering the collection locality, *M. whiteheadi* is more plausible because larva E was collected from Sg. Mamut on the southern slope of Mt. Kinabalu. This river is close to Poring where we collected *M. whiteheadi*.

DISCUSSION

TAXONOMIC CONCLUSIONS

TAXONOMIC RELATIONSHIPS

In the molecular analyses using samples from seven localities, we found three lineages (Mahua, Ulu Senagang and Wario lineages) in the frogs traditionally identified as *M. whiteheadi*. These three lineages did not comprise any monophyletic groups in the evolutionary trees of this genus. Additionally, the genetic distances among these three lineages are relatively large (Ulu Senagang vs. Mahua = 7.8% in 12S and 17.1% in cytb; Ulu Senagang vs. Wario = 8.5%–8.8% in 12S and 16.9% –17.9% in cytb; Mahua vs. Wario = 5.5%–5.8% in 12S and 13.5%–13.8% in cytb). These genetic distances are equal to or larger than those observed between *M. orphnocnemis* and a lineage of *M.* cf. *amoropalamus* (lineages 3 and 4 in Shimada *et al*., 2007), which are distinct sympatric species (4.2%–4.6% in 12S and 15.7%–16.3% in cytb). Considering these results, we conclude that these lineages should be treated as distinct species. Because these taxa are all endemic to Borneo, this discovery contributes to increment of the endemic species ratio in amphibian fauna of this island.

Although we have no DNA samples from Mendolong, we believe that this population belongs to the Ulu Senagang lineage because Stuart's (2008) RAG-1 sequence of "*M. whiteheadi*" collected from this locality (FMNH 238285) was completely identical to that of this lineage. Their specimen and one of our samples from Mendolong (SP 936 = FMNH 238286) were collected in the same night.

Next, we morphologically assigned the remaining specimens to the three lineages. First, the Ulu Senagang lineage is not limited to Kimanis, Mendolong, Sg. Tinuman and Ulu Senagang, but also thought to be distributed in Kepipiyo and Melalap because males characterised by large body size (>50 mm) in the specimens from Kimanis, Mendolong and Ulu Senagang were also observed in these two localities. Melalap and Kepipiyo are both located at the southern Crocker Range close to Ulu Senagang.

Second, the Mahua lineage from Mahua seemed to inhabit at Trus Madi as well, judging from the colour pattern of the upper lip. The dark spots on the upper lip were observed only in specimens from these two localities. Although Mt. Trus Madi is separated from the Crocker Range by the Tambunan plain, Mahua is closest to this mountain among our sampling localities in the Crocker Range.

Third, the Wario lineage from Bario, Poring and Wario seemed to be conspecific with the specimens from Kiau, Melangkap, Monggis and Nalumad. These localities are all located around Mt. Kinabalu, except for Bario, which is in northern Sarawak. The relatively small male body size and the absence of spots on the lip appear to be diagnostic of this lineage and are shared with the specimens from these seven localities. Within this lineage, the samples around Mt. Kinabalu and those from Bario are separated with relatively large genetic distances (2.3%–2.8% in 12S and 6.8%–7.0% in cytb). Two males from Bario seemed to be larger than those from around Mt. Kinabalu, and larvae from Bario had more labial tooth rows than those from Mt. Kinabalu; these characters, however, are all highly variable. We acknowledge that some genetic and morphological variations exist between Bario and Mt. Kinabalu, but we consider them to be intraspecific.

These molecular and morphological assignments do not contradict the results of the character ratio analyses. No significant differences were found within any single lineage (Ulu Senagang lineage = Kepipiyo and Mendolong, Wario lineage = Monggis and Wario). The males of the Ulu Senagang lineage tended to have a smaller head than those of the Mahua and Wario lineages; of the 22 highly supported head relationships, 19 showed this tendency. The males from Mahua tended to have longer limbs, as indicated by all of the eight highly supported limb relationships, and a larger IOD, as shown by the significantly larger IOD of Mahua specimens compared to those from the other four localities. In females, we could not analyse the Ulu Senagang lineage, but the results did not contradict the analyses of males in the Mahua lineage, which had longer limbs than the Wario lineage.

ASIGNMENT OF THE TRUE *MERISTOGENYS WHITEHEADI*

Among the three lineages, we believe that the Wario lineage is the true *M. whiteheadi* for the following reasons. First, the SVLs of the syntypes of *M. whiteheadi* (four males with vocal sacks) were 46 mm (Boulenger, 1887). Our Ulu Senagang males were usually larger than 50 mm and thus cannot be true *M. whiteheadi* (Fig. 5). Next, although the colouration of the syntypes of *M. whiteheadi* is already faded, Boulenger (1887) described this species as having "upper lip and lower surfaces whitish", suggesting that true *M. whiteheadi* does not have any black spots on the upper lip as seen in the Mahua lineage. Thus, we conclude that the Wario lineage represents true *M. whiteheadi*.

The type locality of *M. whiteheadi* was designated only as "Mount Kina Baloo" (Boulenger, 1887), but according to the note by the collector, J. Whitehead, the specimens were acquired during his stay at Melangkap, a village on the western slope of Mt. Kinabalu (Whitehead, 1893). As he collected the specimens on the night of 6 March 1887 using a small torch, the collection site should be not too far from the campsite, most probably at Sg. Panataran. We also collected several specimens from this river (the "Melangkap" samples in this study) and morphologically identified them as the Wario lineage (see above). This fact also strongly supports the assignment of the Wario lineage as true *M. whiteheadi*.

HIND LIMB LENGTH OF *MERISTOGENYS WHITEHEADI*

From our molecular and morphological studies we concluded that the true *M. whiteheadi* should be limited to the Wario lineage. Based on this assessment, we now discuss the hind limb length of *M. whiteheadi*. Earlier studies concerning hind limb length of *M. whiteheadi* discussed whether the tibia-femoral joint reaches the tympanum when the hind limb is pressed forward along the body (Boulenger, 1887, 1891; Mocquard, 1890, 1892). Inger & Gritis (1983) first measured the TL of *M. whiteheadi* and showed that this species has quite short hind limbs (TL 66.5%–68.3% of the SVL in males) compared to other species. This view has been followed by subsequent workers and in Matsui's (1986) key index, *M. whiteheadi* was separated from *M. poecilus* in having a TL <70% of the SVL (>72% of the SVL in *M. poecilus*). In our study, the tibia-femoral joint tended to reach the tympanum in males, but usually did not do so in females. This supports Mocquard (1890, 1892) for males and Boulenger (1887, 1891) for females. In Fig. 6, we plotted the TLs of some *Meristogenys* species against their SVLs. This figure clearly shows that *M. kinabaluensis* has a shorter tibia than any other *Meristogenys* species. Among the remaining species (the *M. jerboa* complex), *M.*

stigmachilus and *M. poecilus* tend plot above the TL/SVL = 0.72 line, whereas *M. orphnocnemis*, *M. phaeomerus* and *M. whiteheadi* usually plot below this line. After all, among *Meristogenys*, *M. whiteheadi* is one of the members with shorter tibia, but not as short as in *M. kinabaluensis*. The range shown by Inger & Gritis (1983) seems to be too limited (66 of 76 male samples of our *M. whiteheadi* deviated from their range). This discrepancy might have been due to the small sample size of Inger & Gritis (1983) and the deteriorated condition of their specimens. We examined a paratype in the Museum National d'Histoire Naturelle, Paris (MNHNP 1889 237), and found its hind limbs unnaturally bent, probably due to decalcification of the limb bones. Such deterioration might seriously bias measurements.

RATIO OF FEMALE AND MALE BODY SIZE

Among three species treated in this study, the degree of sexual size dimorphism was relatively smaller in *M. stenocephalus* (a large species) than in *M. stigmachilus* and *M. whiteheadi* (medium-sized species), with a mean female/male SVL ratio of 1.30–1.51 in *M. stenocephalus*, 1.63–1.66 in *M. stigmachilus* and 1.48–1.71 in *M. whiteheadi*. When sexual size dimorphism was assessed in several other congeners, we found that the female/male SVL ratio was significantly negatively correlated with male and female SVLs (Spearman's rank correlation, $\rho = -0.882$ with male SVL and $\rho = -0.732$ with female SVL; $P < 0.05$). The only result for females is shown in Fig. 8. Sexual size dimorphism tends to be larger in small species than in large species, and the variations in dimorphism observed in *M. stenocephalus*, *M. stigmachilus* and *M. whiteheadi* do not contradict to this generic tendency.

Stream-breeding frogs are known to have large sexual size dimorphism because females must keep their body stationary in flowing water during oviposition while carrying a male on their back. In such a situation, relatively small males would be preferably selected to reduce water-flow resistance (Pope, 1931; Liu, 1950; Matsui & Matsui, 1990). Female *Meristogenys* lay their eggs on rock surfaces in rapidly flowing streams (Malkmus *et al*., 2002 and our own observations) and must also be subjected to such selective pressure. Judging from the negative correlation between body size and the extent of sexual dimorphism shown in Fig. 8, the water-flow effect might work more efficiently for small species in this genus. This inference is plausible because a small female supposedly has reduced swimming ability compared to a large female, and therefore would be more sensitive to water flow. Yet, this explanation is based mainly on several hypothetical assumptions, and we require additional information about

swimming force and reproductive behaviour in the genus.

DISTRIBUTION PATTERNS IN *M. WHITEHEADI*-LIKE FROGS

Meristogenys stigmachilus, *M. stenocephalus* and *M. whiteheadi* have never been collected from identical localities. As these three species are similar in adult and larval morphology, they might have similar niches and be unable to co-exist sympatrically. Among these three species, *M. whiteheadi* is collected from northern Sabah (Mt. Kinabalu) and northern Sarawak (Bario) and *M. stigmachilus* and *M. stenocephalus* inhabit the area between. The genetic differentiation observed in *M. whiteheadi* between northern Sabah and northern Sarawak might have been induced by their disjunct distribution, possibly through the presence of the morphologically similar *M. stigmachilus* and *M. stenocephalus*. In Borneo only a few studies of intraspecific genetic variation have been made on amphibians (e.g. Emerson, Inger & Iskandar, 2000; Matsui *et al*., 2007; Inger, Stuart & Iskandar, 2009), and acquisition of such information will lead to a better understanding of the establishment of the unique herpetofauna of this island.

Judging from available data, *M. stigmachilus* is restricted to higher elevations (Mahua, 1063 m; Trus Madi 850 m), in contrast to the other two species, *M. stenocephalus* and *M. whiteheadi*, which have been collected from a wide range of altitudes (*M. stenocephalus*: 380–820 m, mean = 632 m; *M. whiteheadi*: 300–1000 m, mean = 630 m). Malkmus (1994) and Malkmus *et al*. (2002) recorded Liwagu (‘Liwago’ in their spelling; a river near the Kinabalu Park Headquarters; 1500 m) and Mesilau (1800 m) as the altitudinal range of *M. whiteheadi*. However, we could not find any specimens of *M. whiteheadi* from these two areas, although we collected many larval and adult specimens of other *Meristogenys* species from that locale. Examination of numerous specimens kept in Sabah Parks also revealed no record, and we believe these areas are too high for *M. whiteheadi*. Both *M. stenocephalus* and *M. whiteheadi* are distributed around 400–1000 m, but in a river on the western slope of Mt. Kinabalu, *M. whiteheadi* occupies a higher area (Sg. Wario) than *M. stenocephalus* (Sg. Tinuman). Although Mt. Kinabalu is mainly inhabited by *M. whiteheadi*, *M. stenocephalus* is probably distributed in some lowland areas around this mountain, and an altitudinal segregation may exist between these two species.

Meristogenys stenocephalus was mainly collected from the southern part of the Crocker Range, and only Sg. Tinuman was separated from the other collection sites. This situation appears at a glance to be a disjunct distribution as in the case of *M.*

whiteheadi, but we found no genetic differentiation in 12S or cytb between these two areas. In this case, we must note that our sampling localities may have been biased toward relatively higher areas, partly because of the paucity of good collection sites in lower forests, which tend to have been affected by human activity. We suspect that this species is broadly distributed from lowlands to hilly forests in this area, and inhabits (or formerly inhabited) continuously the lowland forest between the southern part of the Crocker Range and Mt. Kinabalu.

Of the five *M. stenocephalus* localities reported in this study, the “Kimanis” site (trail 5 of the 2002 UMS Expedition; Kueh *et al*., 2004) has now been completely destroyed and buried under the mud through the construction of the new Kimanis Road. We could not collect any *Meristogenys* here in 2005. The “Kepipiyo” site was also damaged by fires in the 1990s and replaced by new secondary forest. Although many specimens of *M. stenocephalus* and *M. orphnocnemis* collected here in 1989 were kept in Sabah Parks, we collected only the latter species in 2006. The “Mendolong” site was also damaged by logging activities (P.Y., personal observation). Compared to the other two species, *M. stenocephalus* seems to live closer to human habitation and a special note of its habitat reduction must made to avoid extinction of this species.

Acknowledgements

The Economic Planning Unit (EPU: 40/200/19 SJ. 1110, SJ. 1158, SJ. 2047, SJ. 2285) of Malaysia, the State Government of Sabah, the State Government of Sarawak, Sabah Parks, and The Forest Department, Sarawak (NPW.907.4.2(III)-68) granted permission for fieldwork. The University of Malaysia Sabah, the Japan International Cooperation Agency (JICA), Sabah Parks, and the Forest Department, Sarawak kindly provided all the facilities for conducting the research. We thank A. H. Ahmad, L. Apin, K. Araya, K. Eto, Y. Hashimoto, T. Hayashi, T. Hikida, N. Koike, K. B. Kueh, D. Labang, M. B. Lakim, M. Maryati, A. Mori, J. Nais, K. Nishikawa, T. Tachi, A. Takahashi, and G. Vu for help in the field, as well as N. Kuraishi, M. Matsubara, T. Matsuiki, K. Nakura, N. Yoshikawa, and staffs of the office of practical education in Faculty of Bioenvironmental Studies, Kyoto Gakuen University for help in the laboratory. We are also indebted to all the collectors of specimens examined in this study; O. Bickford, R. F. Inger, R. Stuebing, F.-L. Tan, and the staff of Zoology unit of Sabah Parks. R. F. Inger also gave a precious comment to our manuscript. We also thank A. Ohler and A. Dubois (MNHNP) for allowing M. M. to examine specimens under their care. This research was partly supported by a fellowship of Japan Society for the Promotion of Science (JSPS) to T.S. and Grants under The Monbusho/JSPS Scientific Research

Programs (Nos. 01041051, 02041051, 03041044, 04041068, 10041166, 15370038) to M.M.

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Figure legends

Fig. 1. Map of Borneo showing the localities where sampling of *M.* cf. *whiteheadi* (closed markings) and other congeneric species (open circles) was conducted. A square=Mahua lineage; triangles=Ulu Senagang lineage; asterisks=Wario lineage; closed circles=*M.* cf. *whiteheadi* without molecular data. 1, Melangkap; 2, Sg. Tinuman; 3, Wario; 4, Monggis; 5, Nalumad; 6, Poring; 7, Mesilau; 8, Liwagu; 9, Kiau; 10, Mahua; 11, Trus Madi; 12, Kimanis; 13, Melalap; 14, Ulu Senagang; 15, Kepipiyo; 16, Mendolong; 17, Bario; 18, Lanjak Entimau; 19, Matang. KNP and CRNP indicate the Kinabalu National Park and Crocker Range National Park, respectively.

Fig. 2. Profiles of *M.* cf. *whiteheadi.* Patterns of upper lip were separated into five types; A, pattern 1-a (several large black spots similar to those of lower lip); B, pattern 1-b (irregular black blotches smaller than lower lip spots); C, pattern 2 (uniformly black); D, pattern 3 (uniformly gray); E, pattern 4 (uniformly white). Specimens vouchers; A, BORNEENSIS 12560 from Mahua; B, BORNEENSIS 12512 from Mahua; C, BORNEENSIS 23302 from Wario; D, BORNEENSIS 23340 from Wario; BORNEENSIS 12810 from Ulu Senagang.

Fig. 3. Bayesian tree of a 957-bp sequence of mtDNA for haplotypes of *M.* cf. *whiteheadi* and its allies. Numbers above or below branches represent bootstrap support with 500/2000 replicates for ML/MP inference. Nodes with asterisks indicate significant support (>95%) by Bayesian inference. The number of adult and larval specimens of each haplotype is shown in parentheses. BA = Bario, KI = Kimanis, MA = Mahua, PO = Poring, TI = Tinuman, US = Ulu Senagang, and WA = Wario. Lin. 1, 3, 4 indicates three distinct lineages found in *M. amoropalamus.*

Fig. 4. Bayesian trees of 5993-bp sequence of mtDNA (left) and 3736-bp of nu DNA (right) for haplotypes of *M.* cf. *whiteheadi* and its allies. Numbers above or below branches represent bootstrap support with 500/2000 replicates for ML/MP inference. Nodes with asterisks indicate significant support (>95%) by Bayesian inference. 3. Lin. 1, 3, 4 indicates three distinct lineages found in *M. amoropalamus.*

Fig. 5. Comparisons of snout-vent length (SVL, in mm) of *M.* cf. *whiteheadi.* Hatched boxes ($n \geq 5$) and closed circles ($n < 5$) indicate male, while open boxes ($n \geq 5$) and circles indicates ($n < 5$) female. Crosses indicate juveniles. Horizontal bars,

vertical bars, and boxes indicate the ranges, means, and 2SE of SVL, respectively. A vertical dotted line indicates SVL = 50 mm.

Fig. 6. Plots of tibia length (TL, in mm) against SVL of nine species of *Meristogenys*. Two lines indicate TL/SVL=0.70 and 0.72. A, *M. orphnocnemis*; B, *M. phaeomerus*; C, *M. jerboa*; D, *M. amoropalamus*; E, *M. poecilus*; F, *M. whiteheadi* from Monggis (closed circles), Wario (open circles), Nalumad (gray circles), Melangkap (gray squares), Kiau (gray triangles), Poring (crosses), and Bario (asterisk); G, *M. stigmachilus* from Mahua (closed circles) and Trus Madi (open circles); H, *M. stenocephalus* from Mendolong (closed circles), Kepipiyo (open circles), Kimanis (gray circles), and Melalap (crosses);.I, *M. kinabaluensis*.

Fig. 7. Adults and larvae of three *Meristogenys* species treated in this study. A-B, *M. stigmachilus* (BORNEENSIS 12512 and 03B1 from Mahua); C-D, *M. stenocephalus* (B12808 and 05B217 from Ulu Senagang); E-F, *M. whiteheadi* (B22971 and 05B209 from Wario). Scale bar = 10 mm.

Fig. 8. Plots of male/female SVL ratio against female SVL; open circles = *M. whiteheadi*, gray circles = *M. stigmachilus*, crosses = *M. stenocephalus*, squares = *M. kinabaluensis*, closed circles = other species of the *M. jerboa* species group.

Table 1. Locations and altitudes of collection locality examined in this study. Sg = Sungai, meaning “River” in Malay. Numbers correspond to locality numbers in Fig. 1.

No.	Location	Altitude (m)
1	Melangkap, Sg. Panataran, Kota Belud District, Sabah	310
2	Sg. Tinuman, Sayap, Kota Belud District, Sabah	750
3	Wario, Sg. Wario, Kota Belud District, Sabah	950
4	Monggis, Sg. Kopuakan, Kota Marudu District, Sabah	300
5	Nalumad, Sg. Mokodou, Kota Marudu District, Sabah	450
6	Poring, Sg. Kipungit I, Ranau District, Sabah	500
9	Kiau, Sg. Kadamaian, Kota Belud District, Sabah	900
10	Mahua, Sg. Mahua, Tambunan District, Sabah	1063
11	Trus Madi, Sg. Rompon and Sg. Pergas, Tambunan District, Sabah	850
12	Kimanis, Sg. Kimanis, Papar District, Sabah	820
13	Melalap, Sg. Melalap, Tenom District, Sabah	700
14	Ulu Senagang, Sg. Senagang, Tenom District, Sabah	550
15	Kepipiyo, Sg. Kilanpun or Sg. Purulon, Tenom District, Sabah	380
16	Mendolong, Sg. Mendolong, Sipitang District, Sabah	590
17	Bario, Baram, Sarawak	1000

TABLE 2. The number of base pairs (bp), variable sites (vs), and parsimony informative sites (pi) for DNA fragments examined in this study.

	bp	vs	pi
12S	931	303	161
16S	1607	525	275
ND1	973	452	312
ND2	1038	540	340
tRNAs	410	119	49
Pseudogene	74	5	2
cytb	960	411	318
POMC	583	98	23
RAG1	783	115	36
RH1	247	27	5
SLC8A3	1063	91	20
NCX1	1060	123	31

Table 3. Results of the Templeton test and SH test. The best tree (1) in MP (Templeton test) and ML (SH test) was compared with four trees under constraints (2-5). Asterisks indicate significant difference.

Templeton test

Tree number	Constraints	Length	P
1	no constraints	5760	
2	Mahua + Ulu Senagang + Wario lineages	5815	0.0009*
3	Mahua + Ulu Senagang lineages	5797	0.0021*
4	Ulu Senagang + Wario lineage	5811	0.0003*
5	Mahua + Wario lineage	5764	0.7548

SH test

Tree number	Constraints	Likelihood	P
1	no constraints	-31041.16	
2	Mahua + Ulu Senagang + Wario lineages	-31073.08	0.014*
3	Mahua + Ulu Senagang lineages	-31066.17	0.036*
4	Ulu Senagang + Wario lineage	-31071.09	0.012*
5	Mahua + Wario lineage	-31044.40	0.612

Table 4. Comparisons of snout-vent length (SVL: means ± 2SE, followed by ranges in parenthesis, in mm) and percentage ratios of each of the other character dimensions to SVL (medians, followed by ranges in parenthesis) in *M.* cf *whiteheadi*. Names of localities with sequenced specimens were shown in bold. Specimens without sequences were assigned to each type based on morphological characters.

	Male												
	Mahua lineage		Ulu Senagang lineage				Wario lineage						
	Mahua N=11	Trus Madi N=2	Kepipiyo N=9	Melalap N=2	Mendolong N=19	**Ulu Senagang** N=1	**Bario** N=2	Kiau N=1	Melangkap N=4	Monggis N=6	Nalumad N=1	**Poring** N=1	**Wario** N=56
SVL	46.6 ± 1.3 (43.3-50.0)	46.0 (45.3-46.7)	57.2 ± 1.2 (53.0-59.4)	52.3 (51.3-53.3)	52.8 ± 1.0 (48.0-57.5)	60.4	50.9 (50.8-51.0)	42.7	44.8 ± 1.6 (43.2-48.6)	45.1 ± 2.4 (42.0-50.4)	41.9	49.8	43.6 ± 0.5 (39.4-47.2)
HL	41.3 (39.4-43.4)	42.7 (42.4-43.0)	40.1 (38.9-42.8)	39.9 (39.4-40.4)	40.5 (37.3-42.9)	40.2	40.3 (40.0-40.6)	41.9	41.3 (40.2-43.0)	41.8 (41.0-45.0)	40.3	41.0	41.7 (39.6-44.7)
S-NL	6.8 (6.5-7.4)	6.5 (6.4-6.6)	6.5 (5.1-7.1)	6.0 (5.5-6.6)	7.0 (5.2-7.8)	7.1	7.3 (7.1-7.5)	7.3	7.9 (7.2-8.8)	7.1 (6.5-8.3)	7.2	6.8	7.1 (5.7-8.6)
N-EL	8.2 (7.8-8.9)	8.4 (7.7-9.0)	8.8 (7.8-9.4)	8.9 (8.6-9.2)	8.6 (7.3-9.7)	8.8	8.3 (8.2-8.5)	8.2	8.4 (7.6-9.6)	8.3 (8.0-8.7)	7.4	7.8	8.4 (7.7-9.7)
SL	16.6 (15.4-17.8)	18.1 (17.7-18.6)	17.0 (16.2-17.5)	16.6 (16.5-16.8)	17.3 (15.9-18.4)	16.7	16.6 (16.3-16.9)	17.3	17.4 (16.1-18.2)	17.4 (16.6-18.6)	16.0	15.1	17.4 (15.6-18.8)
EL	16.1 (15.2-17.2)	16.4 (15.2-17.6)	15.8 (14.7-17.7)	16.5 (15.9-17.0)	15.8 (13.6-17.6)	15.1	16.6 (15.6-17.6)	16.2	17.0 (16.0-18.0)	17.0 (16.4-19.5)	15.0	16.7	16.8 (14.3-19.1)
T-EL	2.7 (2.0-3.6)	2.8 (2.4-3.3)	2.6 (1.9-3.7)	2.3 (1.8-2.8)	2.6 (1.9-3.3)	3.5	2.8 (2.0-3.5)	3.0	2.5 (2.1-2.7)	2.2 (1.4-3.1)	3.1	4.0	2.7 (1.9-3.8)
TDv	10.4 (9.6-11.4)	9.6 (9.3-9.9)	8.5 (8.0-9.6)	8.9 (8.6-9.2)	8.9 (8.4-10.1)	8.6	8.8 (8.3-9.4)	9.4	10.0 (9.6-10.4)	9.5 (8.3-10.3)	10.3	7.8	9.8 (8.7-10.9)
TDh	9.9 (8.6-10.5)	10.3 (9.5-11.1)	7.4 (6.6-9.6)	8.1 (7.9-8.4)	8.0 (6.8-8.9)	8.3	8.1 (7.7-8.4)	8.9	9.9 (8.6-10.5)	8.7 (8.3-9.1)	10.5	6.6	9.2 (7.9-10.8)
HW	35.3 (33.6-36.4)	35.7 (35.3-36.0)	34.4 (32.7-36.4)	32.8 (32.6-32.9)	32.9 (31.1-35.2)	32.3	33.2 (33.1-33.3)	34.9	34.4 (33.6-35.8)	35.5 (34.0-36.8)	34.8	34.5	35.9 (32.8-37.8)
IND	11.3 (10.0-12.2)	11.2 (11.1-11.3)	10.7 (9.9-11.8)	11.0 (10.9-11.1)	11.2 (10.2-11.8)	10.1	10.3 (9.6-11.0)	11.5	11.4 (10.5-12.0)	11.0 (10.7-12.1)	11.5	10.4	11.3 (10.2-12.3)
IOD	9.4 (8.6-9.8)	8.3 (8.2-8.4)	8.4 (7.0-9.1)	8.6 (8.4-8.8)	8.3 (6.9-10.0)	8.4	8.3 (8.0-8.5)	9.1	8.6 (8.2-8.8)	8.1 (7.2-8.9)	8.6	8.6	8.7 (7.3-9.9)
UEW	10.4 (9.7-11.3)	11.1 (11.0-11.1)	10.2 (9.7-11.6)	9.9 (9.6-10.3)	10.4 (9.4-11.6)	10.9	10.0 (10.0)	10.1	9.9 (9.5-11.3)	11.5 (10.5-12.8)	9.8	9.8	10.9 (8.4-12.0)
FLL	69.3 (66.7-75.1)	70.5 (67.5-73.5)	67.5 (63.2-72.6)	-	67.6 (63.1-73.1)	65.2	65.4 (64.2-66.7)	-	72.5 (69.9-74.4)	68.0 (66.0-73.4)	70.4	68.5	68.4 (63.4-72.7)
LAL	53.7 (52.7-56.0)	54.0 (52.7-55.4)	51.8 (49.2-54.4)	51.1 (51.1-51.2)	51.5 (47.5-54.0)	51.7	50.1 (48.0-52.2)	52.9	51.6 (48.4-53.3)	51.3 (50.0-54.5)	52.0	52.8	52.9 (48.7-56.7)
HAL	30.9 (29.3-32.9)	30.7 (29.3-32.0)	29.7 (28.7-30.5)	28.1 (27.0-29.2)	29.2 (26.8-32.1)	30.0	28.8 (27.4-30.2)	31.1	28.8 (26.5-29.7)	29.9 (29.5-32.2)	31.0	29.1	29.8 (28.2-33.7)
HLL	216.1 (211.7-225.2)	212.0 (207.1-217.0)	210.6 (202.0-219.4)	203.9 (196.9-210.9)	208.3 (191.2-222.8)	210.8	213.4 (212.4-214.4)	193.9	205.6 (198.8-207.4)	205.4 (202.5-224.9)	212.6	213.3	208.7 (198.2-223.9)
THIGH	63.9 (60.8-69.3)	65.6 (64.9-66.2)	61.9 (59.2-66.7)	62.5 (62.0-63.0)	62.1 (57.4-66.5)	60.9	62.6 (62.4-62.8)	53.2	61.3 (60.1-62.5)	65.3 (62.5-67.8)	64.4	63.5	62.5 (58.7-67.3)
TL	72.4 (70.7-76.4)	68.3 (66.7-70.0)	70.9 (69.2-74.9)	70.2 (69.6-70.7)	70.0 (65.1-74.1)	71.7	71.5 (70.4-72.6)	68.4	68.6 (67.6-70.9)	72.7 (68.7-77.4)	71.6	72.3	69.8 (65.8-74.6)
FL	59.2 (55.8-61.7)	58.1 (56.3-59.8)	57.1 (52.6-60.7)	54.7 (53.6-55.7)	55.6 (52.3-58.4)	55.8	59.8 (58.1-61.6)	60.7	54.0 (53.7-56.0)	58.1 (54.2-60.1)	58.2	56.6	57.5 (52.9-61.0)

Table 4. Continued

	Female								
	Mahua lineage		Ulu Senagang lineage			Wario lineage			
	Mahua N=5	Trus Madi N=3	Kepipiyo N=1	Mendolong N=1	**Ulu Senagang** N=1	**Bario** N=2	Kiau N=1	**Poring** N=3	**Wario** N=11
SVL	77.3 ± 2.7 (72.1-79.6)	75.1 (69.2-79.6)	86.6	76.5	78.3	81.1 (80.5-81.6)	73.0	73.6 (72.7-74.6)	74.9 ± 1.3 (71.2-79.3)
HL	40.8 (39.9-42.0)	42.3 (40.1-42.5)	39.0	39.0	40.9	37.8 (37.4-38.3)	41.0	39.0 (38.2-39.5)	40.8 (38.4-41.9)
S-NL	6.5 (6.2-6.8)	7.0 (6.8-7.1)	5.9	6.0	6.1	6.3 (6.2-6.4)	7.3	6.7 (5.8-6.8)	6.4 (5.6-7.6)
N-EL	7.8 (7.7-8.5)	7.9 (7.7-8.8)	8.8	8.6	8.3	8.1 (8.0-8.3)	8.5	8.7 (8.4-8.9)	8.1 (7.6-8.9)
SL	16.2 (15.5-16.4)	16.5 (15.6-18.2)	16.1	16.1	15.6	15.3 (15.0-15.7)	17.7	16.2 (16.1-16.6)	16.3 (15.4-17.3)
EL	14.3 (13.6-14.9)	14.4 (14.3-16.2)	14.4	14.8	14.9	13.7 (13.5-13.9)	14.8	14.3 (14.2-14.9)	14.6 (13.9-15.7)
T-EL	3.6 (3.0-4.0)	4.0 (3.8-4.3)	3.5	2.9	3.7	3.5 (3.3-3.6)	4.0	4.1 (3.6-4.5)	3.7 (3.3-4.9)
TDv	6.7 (6.4-6.9)	7.4 (7.0-7.5)	6.9	6.3	6.9	6.2 (5.8-6.6)	6.7	6.6 (5.9-6.7)	6.9 (6.7-7.7)
TDh	5.9 (5.8-6.3)	6.6 (5.9-6.8)	5.5	5.8	5.6	5.7 (5.1-6.4)	5.6	5.2 (5.0-5.6)	6.0 (5.5-6.9)
HW	35.8 (35.2-38.1)	36.6 (35.7-36.8)	35.1	33.5	33.1	33.4 (32.7-34.2)	35.9	35.6 (34.6-36.2)	35.9 (33.8-37.2)
IND	10.2 (9.5-10.3)	10.4 (9.9-10.7)	10.6	10.5	9.7	9.7 (9.7)	10.5	10.1 (9.8-10.3)	10.3 (10.0-11.2)
IOD	8.4 (8.0-8.9)	8.4 (7.4-8.8)	7.9	7.6	8.7	8.5 (7.8-9.1)	8.4	9.5 (9.0-9.5)	8.6 (7.7-9.2)
UEW	9.3 (8.6-9.8)	9.5 (9.2-9.8)	9.2	9.9	10.0	8.4 (8.2-8.7)	9.0	8.6 (8.3-9.8)	9.0 (8.5-10.2)
FLL	66.3 (62.7-70.6)	66.4 (63.9-68.2)	64.2	63.3	63.5	64.0 (62.6-65.3)	67.3	67.3 (65.8-68.8)	64.1 (61.8-68.7)
LAL	53.3 (51.0-54.1)	50.8 (49.0-54.9)	52.2	49.5	50.1	50.7 (50.0-51.4)	51.8	50.3 (50.3-52.3)	50.3 (46.0-52.6)
HAL	30.0 (29.1-30.9)	29.5 (28.3-31.4)	30.1	28.2	27.7	28.5 (28.4-28.6)	29.2	29.4 (27.5-29.6)	28.5 (26.5-29.9)
HLL	217.3 (209.9-225.5)	213.5 (197.7-222.1)	211.4	208.6	200.4	208.3 (208.1-208.6)	207.1	218.3 (209.1-227.5)	206.9 (194.9-214.0)
THIGH	63.3 (58.9-70.3)	64.4 (62.8-68.2)	63.7	61.4	62.3	61.6 (60.1-63.1)	63.8	66.2 (65.9-66.5)	61.9 (58.7-65.8)
TL	73.8 (71.2-78.5)	70.4 (67.7-77.6)	71.8	69.5	70.4	70.3 (69.7-70.9)	70.5	72.9 (70.4-76.2)	68.7 (62.5-73.9)
FL	59.0 (58.2-61.9)	57.1 (55.7-62.7)	57.4	53.5	53.8	58.0 (56.7-59.3)	57.1	58.2 (56.0-59.3)	57.3 (55.1-60.3)

Table 5. Distibutions of upper jaw pattern of *M.* cf. *whiteheadi*. 1-a, large black spots like those on lower jaw; 1-b, irregular black blotches smaller than those on lower jaw; 2, uniformly black; 3, uniformly gray; 4, uniformly white.

		Male					Female				
		1-a	1-b	2	3	4	1-a	1-b	2	3	4
Mahua type	Mahua	10	1				4	1			
	Trus Madi	3					2				
Ulu Senagang type	Kepipiyo			1	3	5			1		
	Melalap				2						
	Mendolong				13					1	
	Ulu Senagang					1					1
Wario type	Bario			1		1		1	1		
	Melangkap				4						
	Monggis				5						
	Nalumad				1						
	Poring				1					3	
	Wario		1	17	35	4			8	3	

Table 6. Summary of characters of larval *Meristogenys* examined in this study.

	Mahua lineage	Ulu Senagang lineage		Wario lineage	
	Mahua	Sg. Tinuman	Ulu Senagang	Bario	Wario
N	3	9	17	10	5
stage	26-27	27-40	26-40	26-30	26-29
surface projections	present	present	present	present	present
labial teeth raw formula	7(4-7)/6(1)	7(4-7)/7(1) -7(4-7)/8(1)	7(4-7)/7(1) -7(4-7)/8(1)	7(4-7)/6(1) -7(4-7)/7(1)	7(4-7)/6(1)
state of lower jaw sheath	undivided	undivided	undivided	undivided	undivided
serrae of jaw sheath					
upper	6-7	10-19	8-16	5-7	5-9
lower	6	8-13	7-12	5-6	5-6
glands					
infraorbital	3-4	1-3	1-6	1-3	1-3
postorbital	3-6	0-2	1-3	1-5	2-5
prespiracular	3-7	0-4	1-9	1-3	2-9
midlateral	2-5	0-4	1-6	1-5	1-9
ventral body	absent	absent	absent	absent	absent
dorsal fin	absent	absent	absent	absent	absent
ventral fin	1-14	0-2	0-6	3-10	0-8

Table 7. Measurements of larval *Meristogenys* examined in this study.

	Mahua lineage	Ulu Senagang lineage		Wario lineage	
	Mahua	Sg. Tinuman	Ulu Senagang	Bario	Wario
TTL					
st. 26-29	27.4 (3) 24.2-30.3	37.9 (2) 36.3-39.4	36.3 ± 1.8 (8) 31.6-40.3	24.2±1.5 (7) 21.6-27.9	27.9 (3) 22.6-31.0
st. 30-33	-	46.4 (2) 43.0-49.7	48.5 ± 3.1 (5) 45.0-53.9	-	-
st. 34-37	-	51.4 (1)	57.5 (2) 54.8-60.1	-	39.3 (1)
st. 38-40	-	64.9±4.4 (4) 59.2-70.1	68.4 (2) 68.9-67.9	-	-
HBL					
st. 26-29	10.4 (3) 9.5-11.5	14.3 (2) 13.6-14.9	13.6 ± 0.6 (8) 12.6-14.7	9.9±0.6 (7) 9.1-11.3	10.3±1.5 (4) 8.2-11.8
st. 30-33	-	17.4 (2) 16.9-17.8	17.7 ± 0.8 (5) 16.4-18.9	12.5	-
st. 34-37	-	19.0 (1)	20.7 (2) 19.3-22.1	-	15.2 (1)
st. 38-40	-	22.9±1.5 (4) 21.2-24.4	23.5 (2) 23.0-24.0	-	-
HBW/HBL	67.8 (67.8-71.0)	68.9 (65.4-72.5)	67.8 (66.4-75.5)	65.3 (64.1-69.3)	71.8 (71.0-73.7)
HBD/HBW	54.9 (53.1-59.4)	56.8 (48.0-64.4)	54.8 (45.9-64.7)	41.6 (37.1-53.7)	46.4 (42.9-49.4)
ED/HBL	14.7 (14.7-14.8)	13.7 (10.7-14.6)	12.8 (10.4-14.0)	14.0 (13.2-16.0)	14.5 (13.6-14.6)
IOL/ED	237.1 (210.2-255.5)	234.3 (208.3-250.0)	241.9 (223.5-292.0)	242.9 (226.7-272.7)	214.3 (206.3-233.3)
ESD/HBL	43.2 (39.9-45.0)	44.8 (41.6-46.9)	42.4 (40.8-46.9)	40.7 (36.6-45.5)	41.5 (37.1-42.6)
INL/IOL	72.1 (62.1-78.5)	66.9 (60.0-74.0)	66.0 (55.7-77.1)	83.3 (73.1-95.5)	66.7 (63.6-69.0)
ODW/HBW	63.1 (62.9-64.4)	57.8 (53.1-62.5)	56.5 (50.3-68.2)	68.8 (61.4-71.6)	59.2 (50.0-62.0)
SNW/HBW	75.7 (74.3-79.9)	68.7 (59.9-78.7)	66.9 (59.3-74.1)	83.3 (78.6-89.8)	71.7 (65.2-74.7)
SUL/HBL	43.2 (37.2-45.6)	48.9 (44.9-50.9)	45.3 (42.8-48.9	44.6 (39.1-47.8)	44.7 (40.0-46.2)
SUW/HBW	102.2 (96.9-102.4)	95.3 (88.1-100.0)	90.1 (83.1-97.6)	95.0 (87.1-101.7)	96.2 (93.3-100.0)
TLL/HBL	162.5 (156.2-172.1)	177.3 (154.4-192.7)	177.9 (150.3-195.2)	145.7 (135.3-155.3)	167.1 (155.9-181.8)
TLD/TLL	24.5 (23.7-26.1)	25.3 (20.8-29.1)	28.1 (23.7-30.2)	27.5 (21.7-29.9)	25.1 (23.9-27.8)

Appendix

Appendix 1. Primers used to amplify mtDNA in this study.

target	name	sequence	reference
12S	12SZ	AAAGGTTTGGTCCTAGCCTT	12Sh in Cannatella et al. (1998)
12S	L1091	AAACTGGGATTAGATACCCCACTAT	12SA-L in Palumbi et al. (1991)
12S	12SF	CATTGCTCGTAATTCCCTGGCG	12SF-H in Goebel, Donnelly, and Atz (1999)
12S	Lnew	TACACACCGCCCGTCACCCTCTT	this study
12S	Hnew	TACCATGTTACGACTTTCCTCTTCT	H1548 in Matsui et al. (2005)
16S	tVal-L	CGTACCTTTTGCATCATGGTC	this study
12S	tVal-H	AAGTAGCTCGCTTAGTTTCGG	this study
16S	L2204new	AAAGTGGGCCTAAAAGCAGCCA	L2188 in Matsui et al. (2006)
16S	H2317	TTCTTGTTACTAGTTCTAGCAT	this study
16S	L2606	CTGACCGTGCAAAGGTAGCGTAATCACT	16L1 in Hedges (1994)
16S	Will6	CCCTCGTGATGCCGTTGATAC	‘6’ in Wilkinson, Drewes, and Tatum (2002)
ND1	L3004	CGACCTCGATGTTGGATCAGG	this study
16S	H3056	CTCCGGTCTGAACTCAGATCACGTAGG	16H1 in Hedges (1994)
ND1	ND1-L	CTYCCTATYCCMTTYTCHAACTTAAA	this study
ND1	ND1-H	CCAATTAGGGCRTATTTRGAGTT	this study
ND2	tIle-L	TAAGGACCTCCTTGATAGGGAG	this study
ND1	tMet-H	AGGAAGTACAAAGGGTTTTGATC	this study
ND2	ND2-L	AAAATWATAGCMTTTTCCTCAAT	this study
ND2	ND2-H	GAHATRAATATDGAGGCRGTTAT	this study
ND2	46RishiAla	TGAGTTGCATTCATGAGATG	Yoshikawa (pers. com.)
ND2	tCysH	TARCACGTGBGGTTGCAAACC	this study
Cytb	L14759	TACAAAAACTTATGGCCCC	this study
Cytb	L15275-2	TTTTCAGTTGATAACGCCAC	this study
Cytb	MVZ28me	TTATGCTTGCGGCTGCAATA	this study
Cytb	H15740	CATGTTARAATGATTGTGTTAGC	this study
POMC	POMC_1	GAATGTATYAAAGMMTGCAAGATGGWCCT	Wiens et al. (2005)
POMC	POMC_7	TGGCATTTTTGAAAAGAGTCAT	Smith, Stephens, and Wiens (2005)

RAG-1	RAG_1F	GCMTTGCTSCCRGGGTATCA	this study
RAG-1	RAG_1R	AGRCARAGKGGTTTGCAGCA	this study
RAG-1	RAG_2F	AAAGCAGTACGTTTCTCATTCA	this study
RAG-1	RAG_2R	TCAATGGACGGAAGGGTTTCAATAA	this study
RH1	Rdp_1F	TACCCTCAGTATTACCTGGCAGA	Shimada et al., 2008
RH1	Rdp_1R	CTTGATCCATTAGTAAACTAATC	Shimada et al., 2008
SLC8A3	SCF_1F	CCATAGARGTCATAACATCACA	this study
SLC8A3	SCF_1R	TTCATRACYTTGCCRTCCAT	this study
SLC8A3	SCF_2F	AAAGCAGTACGTTTCTCATTCA	this study
SLC8A3	SCF_2R	TCAATGGACGGAAGGGTTTCAATAA	this study
NCX1	NCX_1F	ACAACAGTRAGRATATGGAA	this study
NCX1	NCX_1R	CCTTCTGTTTCRATGATCAT	this study
NCX1	NCX_2F	TGGWRTTGTTGARGTCTGGGA	this study
NCX1	NCX_2R	CAKTRTTAACYTCRTGCAT	this study
NCX1	NCX_3F	CACCCTGARAARGAAATGGA	this study
NCX1	NCX_3R	TTTGAAGAAGAYGARAAYTT	this study

Appendix 2. Specimens used in molecular and morphological analysis. BORNEENSIS: University Malaysia Sabah; KUHE: Graduate School of Human and Environmental Studies, Kyoto University; SP: Sabah Parks.

Molecular analysis

M. stigmachilus

Adults (n = 13): BORNEENSIS 12433-12435, 12479, 12512, 12515, 12560-12562, 12620, 12622, 23501, 23502 from Mahua.

Larva (n = 1): BORNEENSIS 03B1 from Mahua.

M. stenocephalus

Adults (n = 2): BORNEENSIS 12809-12810 from Ulu Senagang.

Juveniles (n = 2): BORNEENSIS 12876 from Kimanis and BORNEENSIS 12808 from Ulu Senagang.

Larvae (n = 8): SP 28003_1-28003_3 from Sg. Tinuman, BORNEENSIS 03B409-03B411, 06B21, 06B23_1 from Ulu Senagang.

M. whiteheadi

Adults (n = 33): KUHE 12369 from Bario, KUHE 39352 from Poring, BORNEENSIS 22971, 22976, 22981, 22984-22986, 22990, 22992, 22996, 22997-22998, 23002, 23008-23011, 23014, 23017, 23020, 23041-23044, 23047, 23302, 23305-23306, 23339-23340, 23343, 23348 from Wario.

Larvae (n = 6): 08B1-2, 08B9-10 from Bario, BORNEENSIS 05B192, 05B207 from Wario.

M. amoropalamus (lineage 1): SP 3808 from Sg. Liwagu (larva), Kinabalu Park.
M. amoropalamus (lineage 3): BORNEENSIS 12621 from Mahua.
M. amoropalamus (lineage 4): BORNEENSIS 12623 from Mahua.
M. jerboa: KUHE 12055 from Matang, Sarawak.
M. kinabaluensis: SP21546 from Mahua.
M. maryatiae: BORNEENSIS 8132 from Kimanis, Crocker Range National Park.
M. orphnocnemis: BORNEENSIS 12443 from Mahua.
M. poecilus: KUHE 17416 from Lanjak Entimau, Sarawak.
Rana nigromaculata: KUHE 32995 from Hino, Shiga Pref., Japan.
Fejervarya limnocharis: KUHE uncatalogued specimen from Inuyama, Aichi Pref., Japan.

Morphological analysis

M. stigmachilus

Adults (n = 21): BORNEENSIS 12433-12435, 12479, 12512, 12515, 12560-12562, 12620, 12622, 23501, 23502, SP 2466, 2471, 20350 from Mahua, SP 193, 234, 657-659 from Trus Madi.

Larvae (n = 3): BORNEENSIS 03B1-03B3 from Mahua.

M. stenocephalus

Adults (n = 34): SP 784-785, 2119-2126 from Kepipiyo, BORNEENSIS 9311, 9308 from Melalap, BORNEENSIS 1419-1423, 1433, SP 857, 934-946 from Mendolong, BORNEENSIS 12809, 12810 from Ulu Senagang.

Juvenile (n = 2): BORNEENSIS 12876 from Kimanis and BORNEENSIS 12808 from Ulu Senagang.

Larvae (n = 26): SP 3615_1-3615_2, 3648_1-3648_3, 28003_1-28003_4 from Sg. Tinuman, BORNEENSIS 03B408-03B411, 03B420-03B424, 03B436-03B437, 03B464, 05B215-05B216, 06B021, 06B023_1-06B023_2 from Ulu Senagang.

M. whiteheadi

Adults (n = 89): KUHE 12230, 12369, 53051, 53053 from Bario, SP 301-302 from Kiau, SP 477, 498-500 from Melangkap, SP 145-146, 21142, 21144, 21989-21990 from Monggis, SP 352 from Nalumad, KUHE 39352, SP 265, 267, 2789 from Poring, BORNEENSIS 22971, 22976, 22981, 22984-22986, 22990, 22992, 22996, 22997-22998, 23002, 23008-23011, 23014, 23017, 23020, 23041-23044, 23047, 23302, 23305-23306, 23339-23340, 23343, 23348, SP 1338, 1396, 1398, 1400-1401, 1403-1406, 1408, 1411, 1413, 1415-1418, 1422, 1428, 1430, 1434-1436, 1439-1442, 1445-1446, 1448, 1509-1510, 1757, 2186, 2335, 20867, 20869 from Wario.

Larvae (n = 15): 08B1-08B10 from Mahua, BORNEENSIS 05B192, 05B195, 05B207-05B209 from Wario.

M. amoropalamus (lineage 1: n=12): KUHE 39288, 39363, 39364, 39458, 39460, 39462, BORNEENSIS 22901, 22902, 22930, 22958, SP 21424, 21425 from Mesilau in Mt. Kinabalu, Sabah.

M. jerboa (n=11): KUHE 17093, 17125, 17140, 17151, 17162, 17167, 33604, 33606-33609 from Matang, Sarawak.

M. kinabaluensis (n=8): BORNEENSIS 12481-12484, 12629, 12630, SP 21546, 21547 from Mahua.

M. orphnocnemis (n=57): BORNEENSIS 8827, 8852, 8858, 8859-8863, 8865, 8866, 12436-12444, 12447, 12448, 12464, 12477, 12478, 12517-12519, 12521, 12522, 12563-12570, 12579-12583, 12625, 22590, 22599, 22600, 22602-22604, 22609, 22611, 22613-22618 from Mahua.

M. phaeomerus (n=25): KUHE 17347, 17352, 17353, 17371, 17387, 17393, 17405-17408, 17410-17415, 17422, 17425, 17431, 17438, 17446, 17451, 17458, 17470, 17471 from Lanjak Entimau, Sarawak.

M. poecilus (n=20): KUHE 17303, 17346, 17416, 17423, 17432-17435, 17447-17450, 17466-17469, 17487, 17497, 17498, 17520 from Lanjak Entimau, Sarawak.

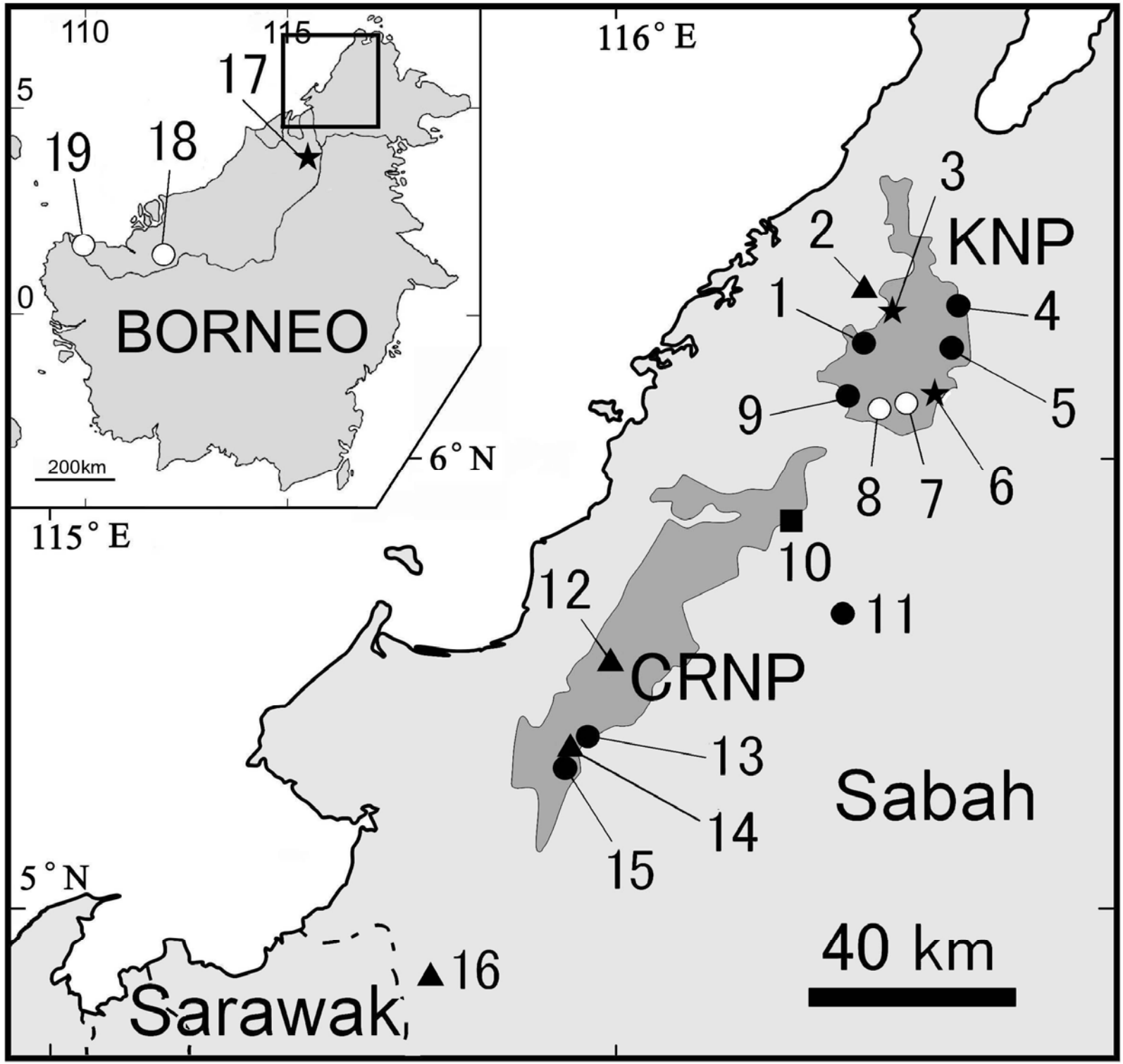
110
115
5
0
17
19
18
BORNEO
200km
6° N
115° E
116° E
KNP
1
2
3
4
5
6
7
8
9
10
11
12
CRNP
13
14
15
16
Sabah
Sarawak
5° N
40 km

Fig. 1

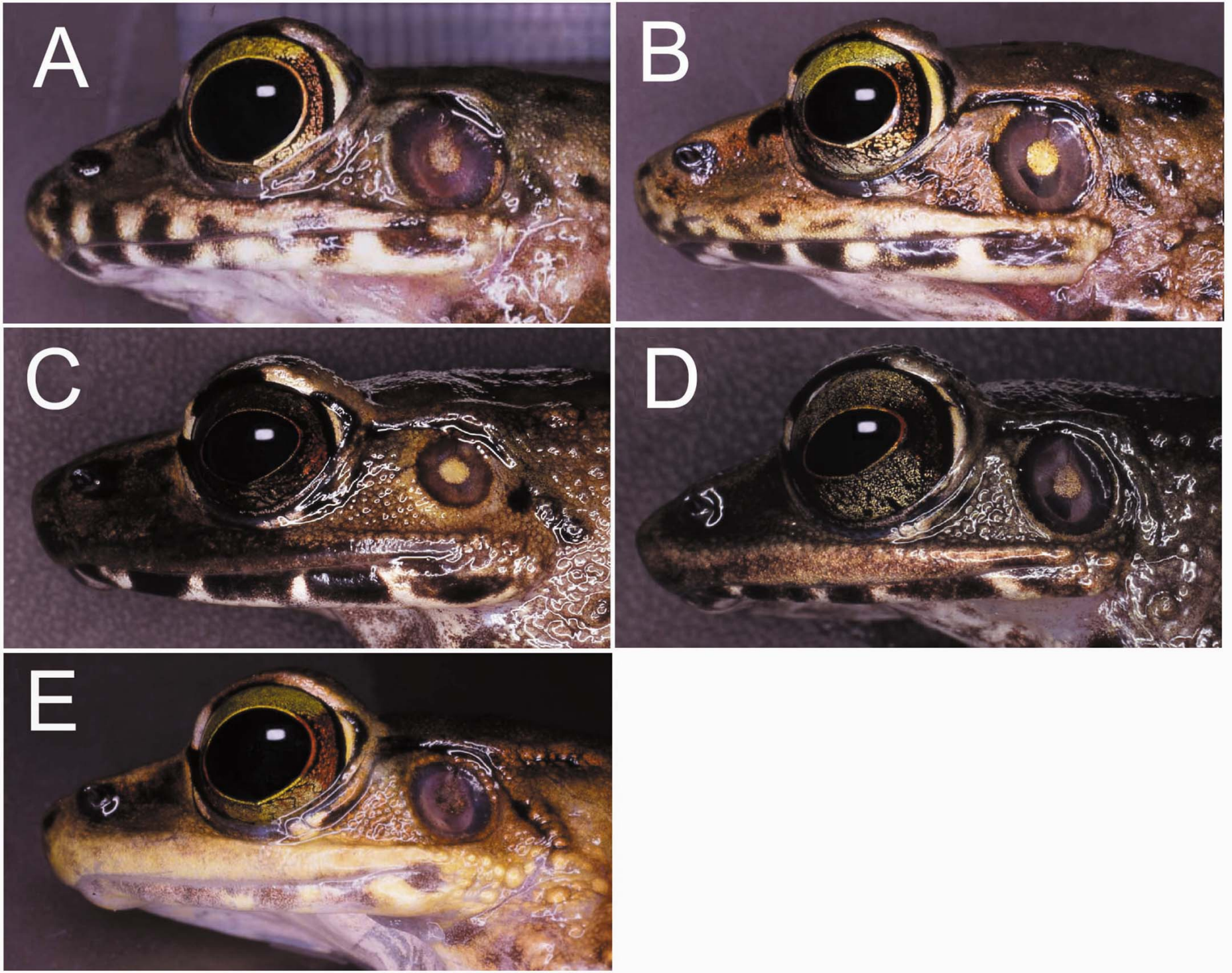

Fig. 2

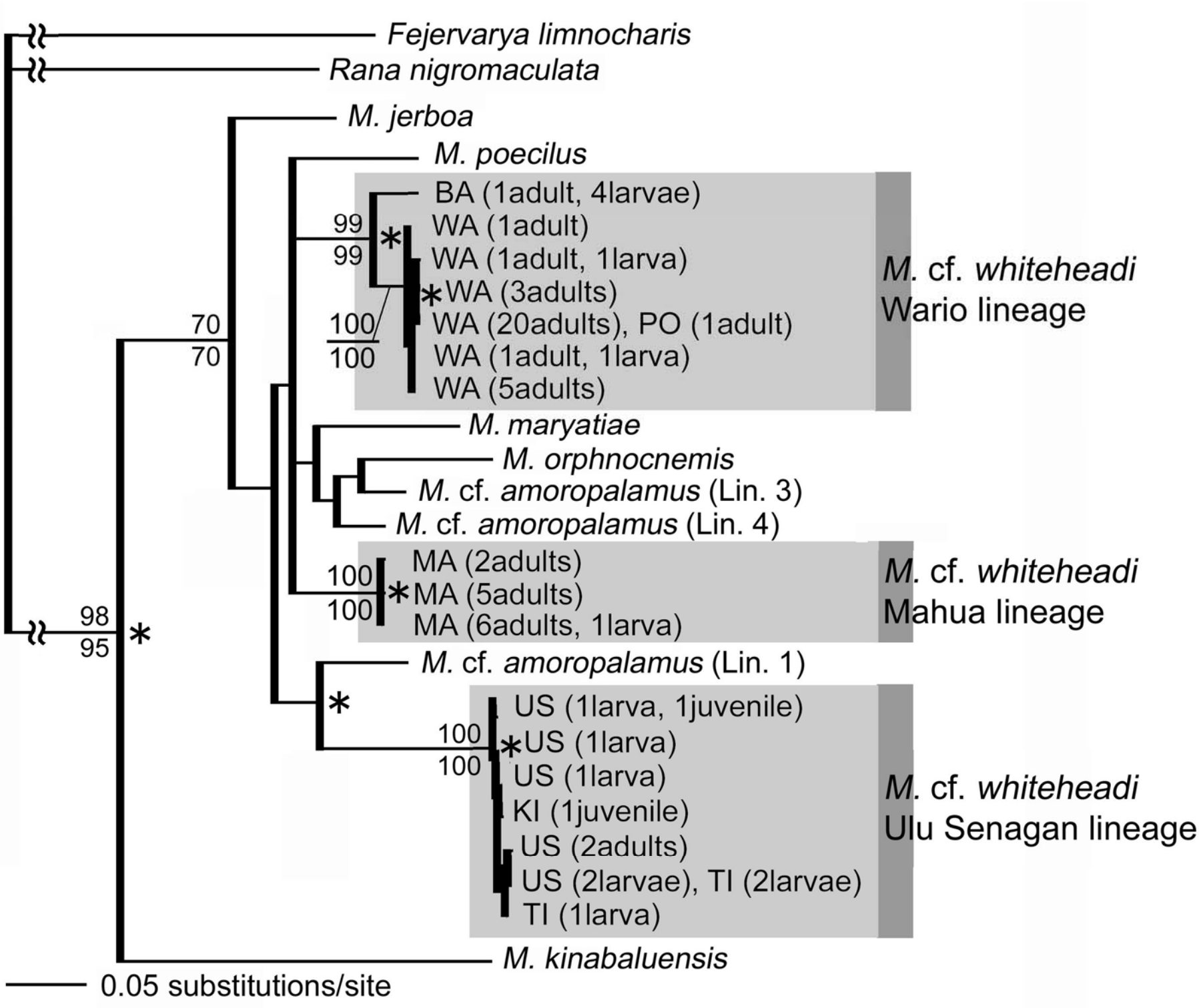
Fejervarya limnocharis
Rana nigromaculata
M. jerboa
M. poecilus
BA (1adult, 4larvae)
WA (1adult)
WA (1adult, 1larva)
WA (3adults)
WA (20adults), PO (1adult)
WA (1adult, 1larva)
WA (5adults)
M. cf. whiteheadi
Wario lineage
M. maryatiae
M. orphnocnemis
M. cf. amoropalamus (Lin. 3)
M. cf. amoropalamus (Lin. 4)
MA (2adults)
MA (5adults)
MA (6adults, 1larva)
M. cf. whiteheadi
Mahua lineage
M. cf. amoropalamus (Lin. 1)
US (1larva, 1juvenile)
US (1larva)
US (1larva)
KI (1juvenile)
US (2adults)
US (2larvae), TI (2larvae)
TI (1larva)
M. cf. whiteheadi
Ulu Senagan lineage
M. kinabaluensis
99
99
70
70
100
100
100
100
98
95
0.05 substitutions/site

Fig. 3

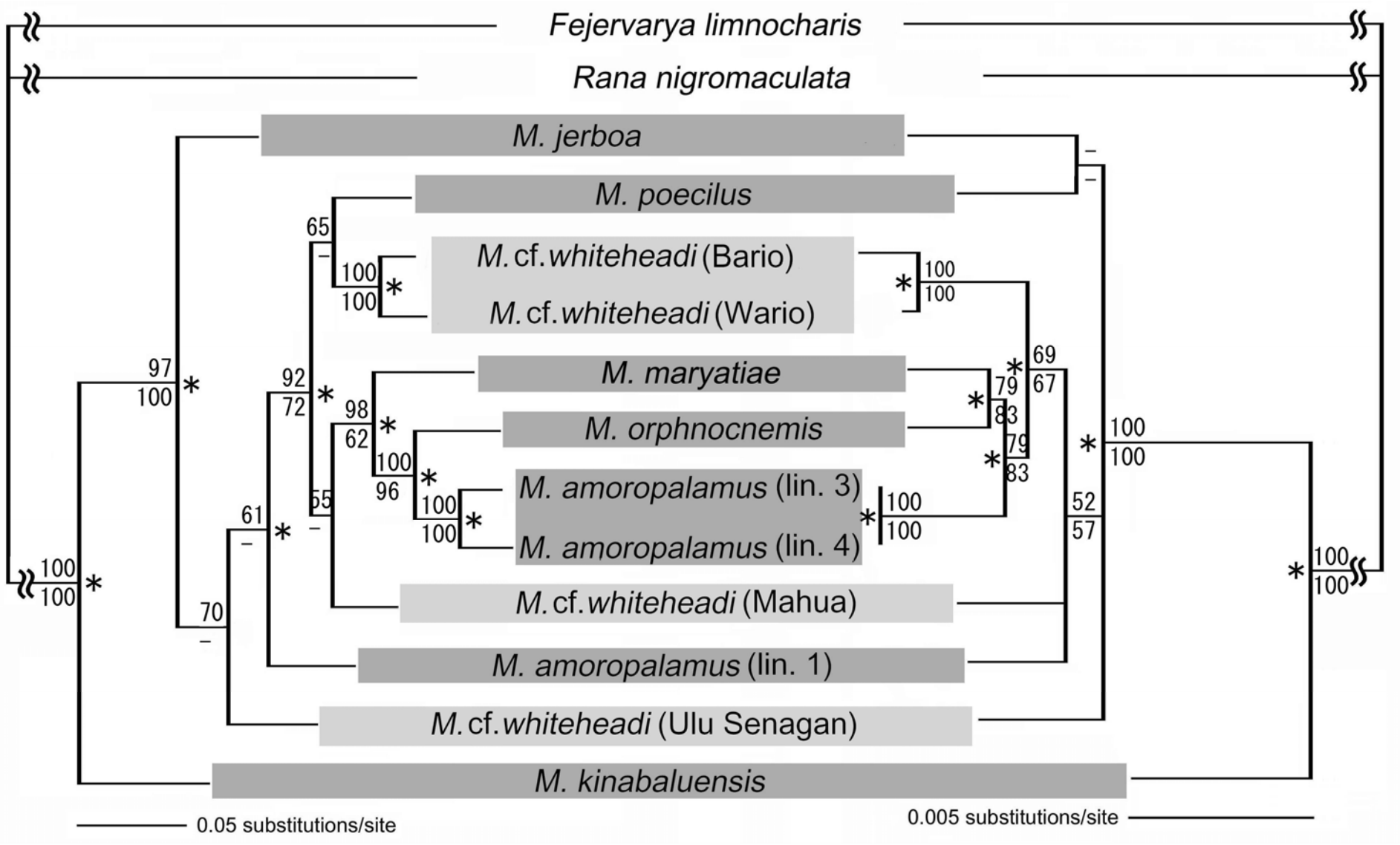
Fejervarya limnocharis
Rana nigromaculata
M. jerboa
M. poecilus
M. cf. whiteheadi (Bario)
M. cf. whiteheadi (Wario)
M. maryatiae
M. orphnocnemis
M. amoropalamus (lin. 3)
M. amoropalamus (lin. 4)
M. cf. whiteheadi (Mahua)
M. amoropalamus (lin. 1)
M. cf. whiteheadi (Ulu Senagan)
M. kinabaluensis
0.05 substitutions/site
0.005 substitutions/site

Fig. 4

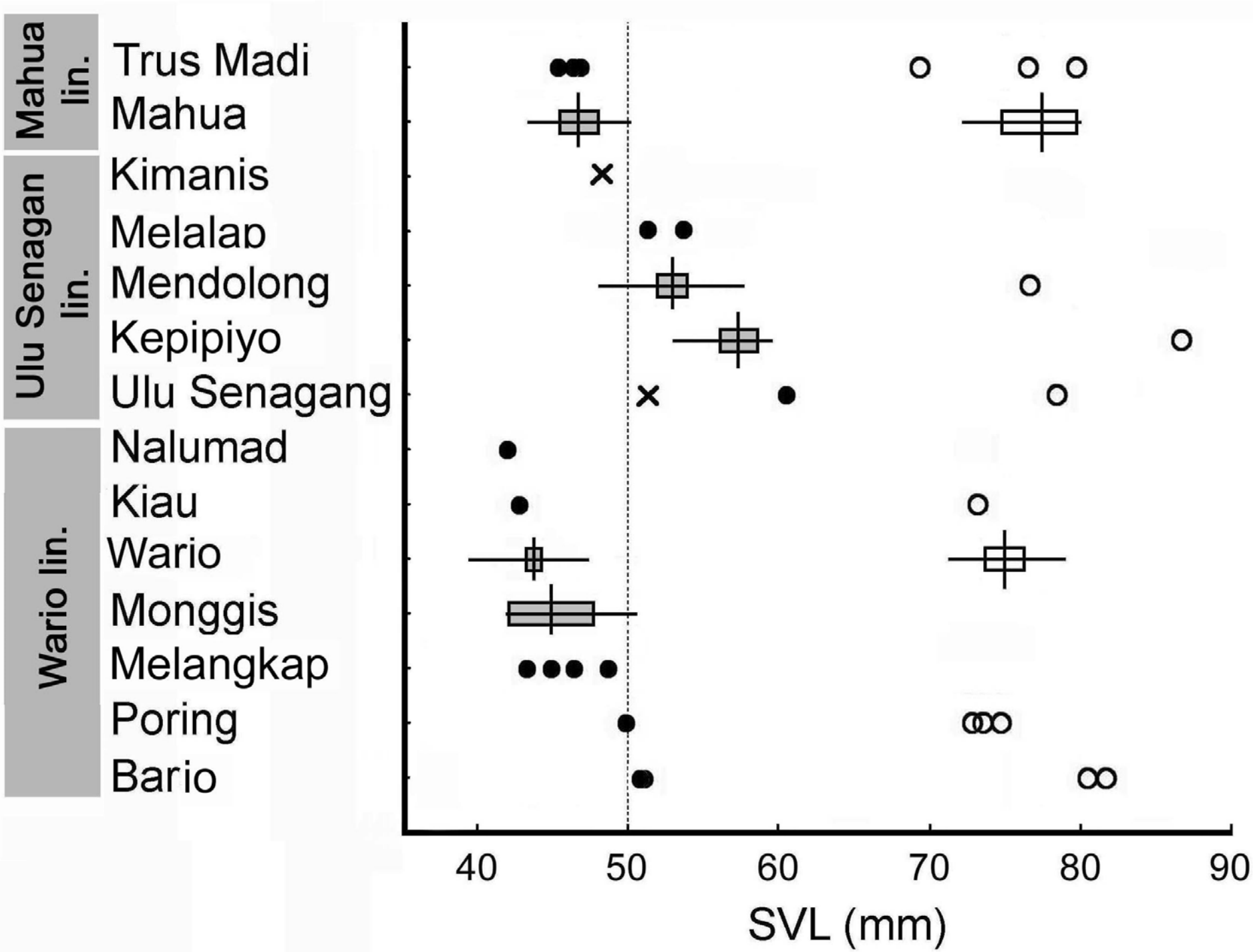
Mahua lin.
Ulu Senagan lin.
Wario lin.
Trus Madi
Mahua
Kimanis
Melalap
Mendolong
Kepipiyo
Ulu Senagang
Nalumad
Kiau
Wario
Monggis
Melangkap
Poring
Bario
40
50
60
70
80
90
SVL (mm)

Fig. 5

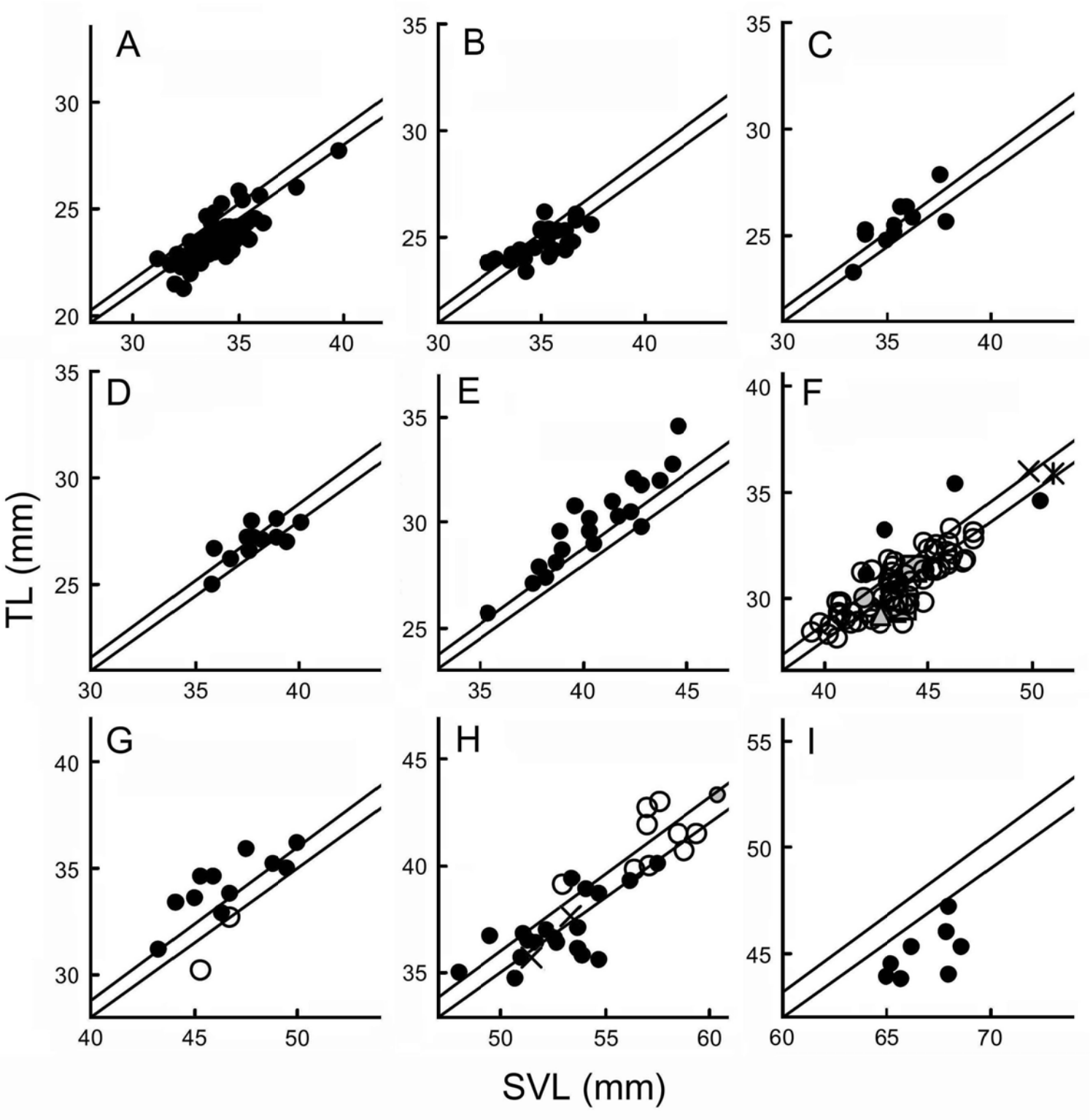

Fig. 6

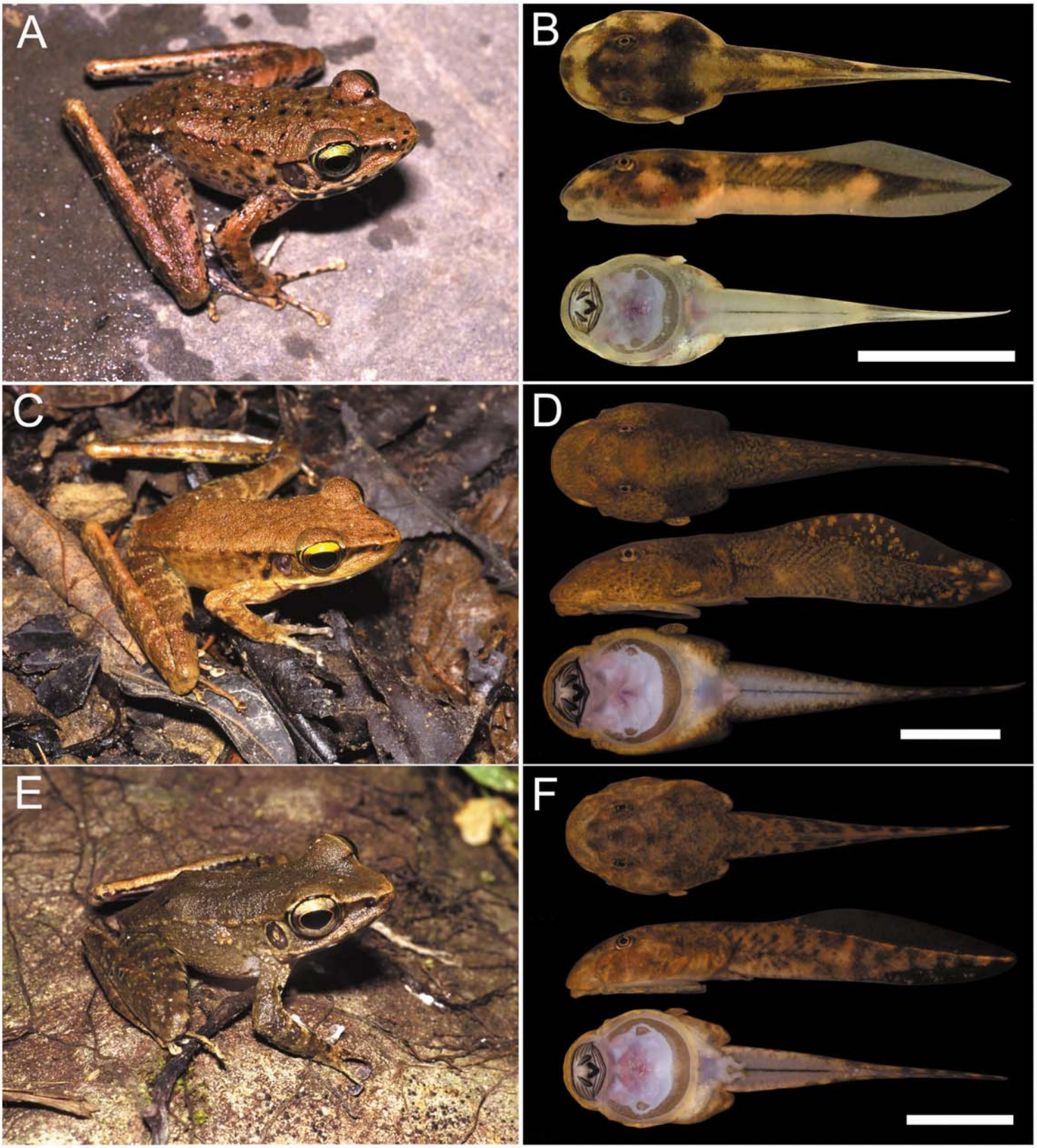

Fig. 7

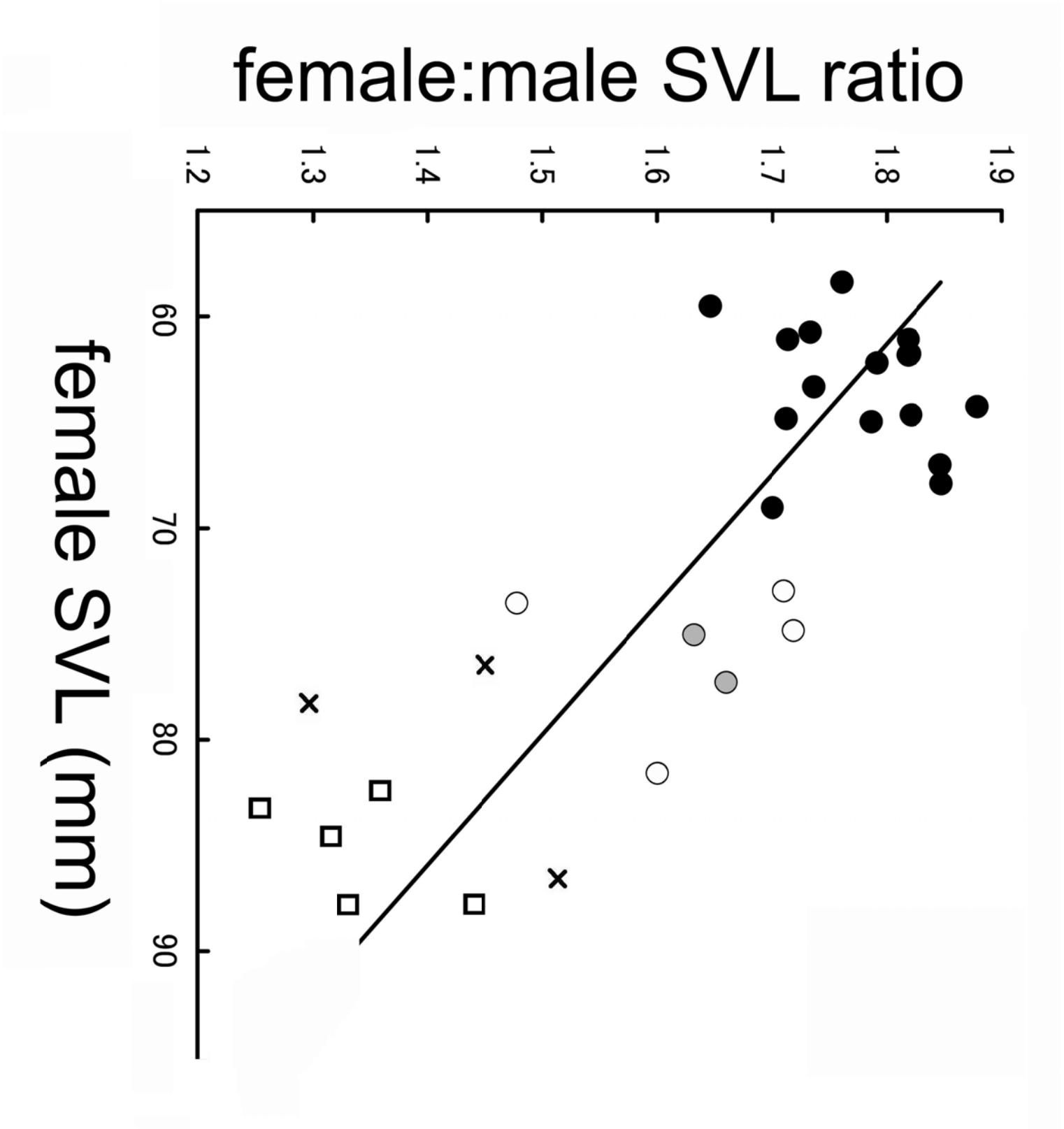

Fig. 8